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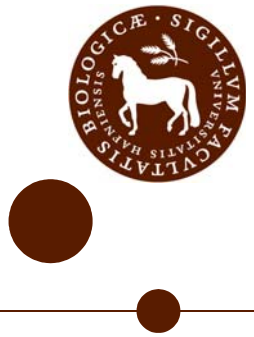

MODELLING CROP ROOT DEVELOPMENT AND NITRATE UPTAKE

ANDERS PEDERSEN

PH.D. THESIS

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LC 2278

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Modelling crop root development and nitrate uptake

Denne afhandling er af Ph.D. Studienævnet ved Det Biovidenskabelige Fakultet for Fødevarer, Veterinærmedicin og Naturressourcer antaget til offentligt at forsvares for den jordbrugsvidenskabelige Ph.D. grad.

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Christian Richard Jensen. Senior Associate Professor, Jordbrugsvidenskab, Det Biovidenskabelige Fakultet, Københavns Universitet, vil fungere som formand for bedømmelsesudvalget.

Preface

This thesis is submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy (Ph.D.) at Copenhagen University. The thesis is the result of a 3-year study at the Plant and Soil Science Laboratory, Department of Agricultural Sciences, Faculty of Life Sciences, University of Copenhagen (formerly the Royal Veterinary and Agricultural University) and Department of Horticulture, Faculty of Agricultural Sciences, Aarhus University (formerly the Danish Institute of Agricultural Sciences). The work was carried out under the supervision of Professor Lars Stoumann Jensen and Section Leader Kristian Thorup-Kristiansen. A third of the Ph.D. was funded by one-year scholarships from the Research School for Organic Agriculture and Food Systems (SOAR). The remainder of the research was partly funded by the Danish Research Centre of Organic Farming (DARCOF) under the programme: *Organic vegetable cultivation methods and use of catch crops* and partly by the European Community Network *EU-Rotate_N* project under Framework 5. I received a grant from 'Studiefonden for Danmarks Jordbrugsvidenskabelige Ph.D. Forening' to cover part of travel expenses to the 37th Biological System Simulation Conference in Beltsville, Maryland, USA.

The thesis is based on three scientific papers (I-III), which are enclosed as appendices. The first paper has been published, second accepted subject for major revision and the third is in preparation.

Paper I

Anders Pedersen, Bjørn M. Petersen, Jørgen Eriksen, Søren Hansen and Lars Stoumann Jensen 2007. A model simulation analysis of soil nitrate concentrations – does soil organic matter pool structure or catch crop growth parameters matter most? *Ecological Modelling* 205:1-2, 209-220.

Paper II

Anders Pedersen, Kristian Thorup-Kristensen and Lars Stoumann Jensen. 2008. Simulating nitrate retention in soils and the effect of catch crops use and rooting pattern. Accepted subject to major revision in *Soil Use and Management.*

Paper III

Anders Pedersen, Kefeng Zhang, Kristian Thorup-Kristensen and Lars Stoumann Jensen. Simulating root density dynamics and nitrogen uptake in the soil profile – A simple approach. *In preparation*.

During the Ph.D. project I attended Ph.D. courses to fulfil the requirements on completion of approved courses and presented my work at different international workshops and conferences with poster and oral presentations.

In conjunction with Paper II, an internet tool for calculating nitrate retention under Danish conditions was developed as a mineral N forecast. Here users select a location in Denmark and add information about soil type, main crop, harvest date, data of sowing or planting of crops in spring. The tool provides users with information on retained nitrate in the root zone on the day of sowing or planting and information on nitrate in deeper soil layers if a shallow or deep-rooted crop is selected. The tool also provides users with the opportunity to see the potential mineral N content by choosing different crop species with different rooting depths. Available at website: *www.planteinfo.dk,* select '*Kvælstof*' then '*Nmin prognonse*' in the menu bar (In Danish).

In conjunction with Paper III, the developed and analysed root model was used in the EUrotate_N model, which is free and available at website: http://www2.warwick.ac.uk/fac/sci/whri/research/nitrogenandenvironment/EUrotateN. The model will be used as a decision support system to optimise nitrogen use in field vegetable rotations across Europe. I developed and improved root development in the atmosphere and plant soil model *Daisy*. The root module description is available in the *Daisy* Program Reference Manual *(website: http://www.dina.kvl.dk/~daisy/ftp/daisy-ref.pdf)* under Part II '*The components*' then Ch. 45 '*Rootdens*' then Sect. 45.5: '*Anders Pedersen*'.

Acknowledgements

My work on this thesis has involved the help of many people in the past three years and I would like to express my gratitude to all of them. Special thanks to my two supervisors, Professor Lars Stoumann Jensen and Section Leader Kristian Thorup-Kristiansen for support throughout the project.

During the project I took part in the European project EU_Rotation_N and I am thankful for inputs and inspiration from the whole group. I especially thank Claas Nendel and Matthias Fink, Institut für Gemüse- und Zierpflancenbau, Grossbeeren, Germany, for discussions about modelling and soil N calculations and Kefeng Zhang, Horticulture Research International, University of Warwick, for excellent coding expertise during the preparation of the root model and inputs on paper III. Thanks to my co-authors for fruitful cooperation during manuscript preparation.

I wish to acknowledge the beneficial inputs from people in the groups around me at Frederiksberg and Årslev: Jesper Luxhøi, Pai Pedas, Andreas de Neergaard, Adrian M. Bollinger and Dorthe Bodin Dresbøll. Further thanks to Sander Bruun for highly scientific discussions on modelling.

Copenhagen University

Frederiksberg, 22 January 2008

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Anders Pedersen (LC 2278)

Summary

Nitrate leaching from agricultural areas is a political and environmental issue at both local scale in Denmark and at global scale. Plant-available nitrogen and nitrate in the rooting zone in the growing season is necessary in order to obtain satisfactory crop yields. However, surplus nitrogen leads to a risk of nitrate losses through leaching and denitrification. In addition to artificial applications of nitrate, nitrate is produced by mineralisation processes in the soil from plant residues and soil organic matter and by nitrification. Therefore nitrate losses can be difficult to control.

This thesis investigates root growth in arable and vegetable crops through construction and improvement of existing models for determining root growth and associated N uptake. The models provide an insight into nitrate dynamics in the soil matrix, and can be used to predict plant yield and N uptake and changes in different soil N pools. Here, the models were used for analysing different physical and biological processes in soil. This was combined with analysis of model construction and parameterisation of crop modules, root sub-modules and soil organic matter pools for predicting nitrate leaching and retention.

The first study analysed the effect of soil organic matter (SOM) module structure and sensitivity of the parameters in the crop modules on nitrate concentration at 1 m depth in the plant soil model *Daisy*. Three different SOM sub-models and two different parameterisations of catch crop sub-modules were analysed. All three SOM modules accurately simulated plant production and nitrogen uptake for cereals. The dynamics of added organic matter and SOM in the two *Daisy* sub-modules were nearly identical, whereas the third sub-module built much more nitrogen into the added organic matter pools. In general, simulated nitrate concentrations at 1 m depth were higher than measured values. Choice of catch crop sub-module had a considerable effect on nitrate concentration and thus potential nitrate leaching, possibly overshadowing more subtle differences produced by the different SOM sub-modules. The simulations in this work showed the importance of applying appropriate intercrop sub-models when simulating rotations with intercropping of grass-clover or undersown catch crops.

The second study analysed nitrate retention during winter in different climate regimes and soil texture classes and the potential of using catch crops to minimise nitrate losses. The model analysed effects of catch crop (*Brassica* and ryegrass (*Lolium perenne*) root growth on nitrate retention, covering three soil types (sand/loamy sand/sandy loam), and three winter precipitation regimes (43 years of data) in a temperate climate representative of Denmark. The sandy soil had a limited ability to retain nitrate in upper soil layers, regardless of precipitation regime and year. With low precipitation, the mean fraction of nitrate retained in the 0-2.0 m soil layer was 0.23 for sand, 0.69 for loamy sand and 0.81 for sandy loam. Simulations showed that catch crops accumulated N in the topsoil layer in plant litter for potential mineralisation in the coming growing season. *Brassica* emptied the 0-0.75 m soil layer of mineral N better than ryegrass. In the 0.75-2.0 m layer, ryegrass still affected the risk of nitrate leaching despite having no roots present, but much less efficiently than *Brassica*, which occupied this layer with roots. In low precipitation years, high nitrate retention occurred in the loamy sand and sandy loam and for a deep-rooted crop planted the following year, access to N was greater where no catch crop had been grown. In years with high winter precipitation, and generally on the sandy soil, catch crops always increased available N in the following spring.

The third study developed a two dimensional root sub-module for calculation of root density, nitrate and ammonium uptake for row crops typically grown in horticultural systems. The model is based on a modification of an existing root density calculation and exploits the abilities of the critical root form parameter to distribute root biomass vertically and horizontally in the soil profile. The root module has other components to account for root growth features, such as specific root length, specific N uptake and different root distribution over the season. The most important parameter in adjusting N uptake from deeper soil layers proved to be root form parameter and the distribution of root biomass. This work provides the potential for more accurate simulation of N uptake by field crops in one- and two-dimensional models.

Previous work on improving root modelling has been limited because of lack of field data and difficulties in applying data from hydroponic systems and pot experiments to belowground processes in real soil. The root model presented here allows crop modelling to be improved with more adequate simulations of root density distributions. This is very

important when using plant models for system analyses of the environmental impact of agriculture and for decision support.

Sammendrag

Udvaskning af nitrat fra det dyrkede areal er både et stort politisk, og miljømæssigt emne, der er meget oppe i tiden lokalt i Danmark såvel som på global plan. Det er en nødvendighed med kvælstof og nitrat i planternes rodzonen i vækstsæsonen for at sikre et højt udbytte af god kvalitet. Et overskud af nitrat kan dog fører til tab i form af udvaskning og denitrifikation. Udover planteproducentens tildeling af nitrat til jorden, bliver nitrat frigivet ved mineraliseringsprocesser af planterester og organisk stof fra jorden og ved nitrifikationsprocesser. Derfor kan nitrattab fra jorden være vanskeligt at kontrollere.

Denne afhandling undersøger rodvækst i land- og havebrugsafgrøder ved forbedring af eksisterende modeller for bestemmelse af rodudvikling og den tilhørende kvælstofoptagelse. Modellerne giver en indsigt i nitratdynamik i jordprofilen og bruges til forudsigelse af udbytte og nitrat optag samt ændringerne i de forskellige modellerede kvælstofpuljer. I dette arbejde er modellerne brugt til analyse af forskellige fysiske og biologiske processer i jorden. Dette indebærer en analyse af modelopbygningen og paramateriseringen af afgrødemoduler, samt modul for rodvækst og puljefordelingen af det organiske stof. Afhandlingen indeholder derudover en analyse af organiskestof puljer og modelparameternes indflydelse på nitratudvaskningen eller tilbageholdelsen.

Det første studie i afhandlingen analyserer betydningen af organisk stof moduls opbygning og følsomheden af parameterændringer i afgrødemoduler på nitratkoncentrationen ved 1 meters dybde i plante og jordmodellen *Daisy*. Tre forskellige opbygninger af organiskstofmodulet og to forskellige paramatiseringer af efterafgrødemodulet blev analyseret. Ved brug af de forskellige organiske stofmoduler blev udbytte og N-optag for vårbyg simuleret tilfredsstillende. Dynamikken i modulet for tildelt organisk materiale og det organiske stof modul var næste identiske i de to *Daisy* relaterede moduler, mens det tredje modul indbygger mere N i modulet for tilført organisk materiale. Generelt var den simulerede nitratkoncentration ved 1 meters dybde højere end den de målte værdier. Valget af efterafgrødemodul havde en mærkbar effekt på nitratkoncentrationen og derfor også udvaskningspotentialet, hvilket vil overskygge de små ændringer forårsaget af de forskellige opbygninger af organiskstofmodul. Simuleringerne i dette arbejde viser betydningen af parametervalg i afgrødemoduler, når

der simuleres sædskiftesekvenser med samvækst af kløver, græs eller undersået rajgræs som efterafgrøde.

Det andet studie analyserer nitratretentionen over vinteren i forskellige klima regimer og teksturklasser og potentialet i retentionen ved brug af to efterafgrøde til at minimere tabet af nitrat. Modellen analyserer effekten af efterafgrødens (*Brassica* og rajgræs) rodvækst på nitrattilbageholdelse. Analysen dækker tre jordtyper som er sandjord, lerblandet sandjord og sandblandet lerjord samt tre forskellige nedbørs regimer, der er lav, middel og høj nedbørs regime over 43 år i et tempereret klima, der repræsenterer Danmark. Sandjorden havde begrænset evne til at tilbageholde nitrat i de øverste jordlag uafhængigt af nedbørsregime og år. Ved lavt nedbørsregime og den gennemsnitlige tilbageholdte fraktion i 0–2.0 meters dybde var resultatet 0.23 for sandjord, 0.69 i lerblandet sand og 0.81 i sandblandet ler. Simuleringerne viste, at brug af efterafgrøder vil akkumulere N i det øverste jordlag som organisk bundet kvælstof i planterester, der frigives løbene efter at være blevet nedmuldet. *Brassica* udtømte jordlaget 0-0.75 m for mineralsk N bedre end rajgræs. I jordlaget 0.75-2.0 m, hvor rajgræs afgrøden ikke har rødder, vil rajgræs stadigvæk kunne mindske nedvaskning af nitrat, men det er dog mindre effektivt end *Brassica*, der har rødder i jordlaget. I det lave nedbørsregime, var der stor tilbageholdelse af nitrat i lerblandet sand og sandblandet ler og med en dybrodet afgrøde året efter, vil der være mere nitrat til rådighed uden brug af efterafgrøde sammenlignet med brug af efterafgrøde. I år med høj vinternedbør og generelt på sandjord, vil brug af efterafgrøder altid øget indholdet af N i jorden næste forår.

I det tredje studie blev der udviklet en todimensional rodmodul til beregning af roddensitet og nitrat- og ammoniumoptag for en række afgrøder, som er typiske for havebrugsområdet. Modellen er baseret på en modifikation af Gerwitz and Page's roddensitetsberegning og udnytter en mulighed for rodformparameter til fordeling af rodbiomassen vertikalt og horisontalt i jordprofilen. Rodmodulet har andre komponenter til at styre andre rodvækstprocesser som specifik rodlængde, specifikt N-optag og forskellig rodfordeling over vækstperioden. Den vigtigste parameter for styring af N optag fra dybere jordlag var rodformparameteren. Dette studie viser potentialet for en mere præcis simulering af N i en- og todimensionale modeller.

Modelling crop root development and nitrate uptake

Tidligere arbejde med udvikling af rod modellering har været begrænset af mangel på data og problemer med at udnytte eksperimentelle data fra vandbaserede systemer og potteforsøg til beskrivelse af rødders udvikling under markforhold. Rodmodellen præsenteret her vil forbedre afgrødemodellering ved en forbedret rodsimulering og fordeling af rødder. Det er meget vigtigt, når man anvender afgrødemodeller til systemanalyse af miljøpåvirkninger af jordbrugssystemet og til brug for beslutningsstøtte af sædskiftesekvenser.

Contents

This thesis is based on the following papers, which are referred to in the text by their Roman numerals:

Paper I Pedersen A, Petersen BM, Eriksen J, Hansen S and Stoumann Jensen L. 2007. A model simulation analysis of soil nitrate concentrations – does soil organic matter pool structure or catch crop growth parameters matter most? *Ecological Modelling* 205:1-2, 209-220.

Paper II Pedersen A, Thorup-Kristensen K and Stoumann Jensen L. 2008. Simulating nitrate retention in soils and the effect of catch crops use and rooting pattern. Accepted subject to major revision in *Soil Use and Management* .

Paper III Pedersen A, Zhang K, Thorup-Kristensen K and Stoumann Jensen L. Simulating root density dynamics and nitrogen uptake in the soil profile – A simple approach. *In preparation.*

List of abbreviations

Symbol	Unit	Description
Plant and Root model		
a_x	-	Form parameter, vertical
a_z	-	Form parameter, horizontal
α	-	Distribution ratio
b	-	Buffer power of the soil
$c_{NH_4^+}$	[kg N ha^{-1}]	Ammonium concentration
$c_{NO_3^-}$	[kg N ha^{-1}]	Nitrate concentration
$c_{\min\_NH_4^+}$	[kg N ha^{-1}]	Ammonium unavailable for plant uptake
$c_{\min\_NO_3^-}$	[kg N ha^{-1}]	Nitrate unavailable for plant uptake
c_{min}	-	Minimum concentration influx
c	-	Concentration of influx ion
β	-	Algometric growth ratio
γ	[kg DM kg^{-1} (CH_2O)]	Conversion factor
C	[M]	Concentration in soil solution
DD	[°C]	Degree days
D_s	[$cm^2 s^{-1}$]	Diffusion coefficient
$F_{g,d}$	[Kg(CH_2O) $m^{-2} d^{-1}$]	Canopy gross photosynthesis
J^*	[mass of nutrient /biomass root]	Uptake rate
J^*_{max}	[mass of nutrient /biomass root]	Maximum ion uptake
K_m	[M]	Michaelis constant
k_{rz}	[m day^{-1} °C^{-1}]	Vertical root penetration rate parameter
k_{rx}	[m day^{-1} °C^{-1}]	Horizontal root penetration rate parameter
K_f		N uptake factor
kN		N uptake factor
L_0	[m m^{-3}]	Root density at surface
L_r	[m m^{-2}]	Total root length
L_z	[m m^{-3}]	Root density at soil depth z
m_N		Parameter to adjust daily N uptake.
N_{demand}	[kg N ha^{-1}]	Nitrogen demand calculated daily
$N_{pot}(NH_4^+)$	[kg ammonium-N ha^{-1}]	Potential ammonium uptake
$N_{pot}(NO_3^-)$	[kg nitrate-N ha^{-1}]	Potential nitrate uptake
q	-	Declining part in root density below calculated root depth
RL_rW_r	[m t^{-1}]	Relative growth rate for root length
RGW_s	[kg t^{-1}]	Relative growth rate for shoot
r	[m]	Radial distance
r_0	[m]	Root radius
r_m	[Kg(CH_2O) kg^{-1}DM d^{-1}]	Maintenance respiration coefficient at actual temperature
R_x	[m]	Root penetration into width
R_z	[m]	Vertical root depth
$R_{z\text{-max}}$	[m]	Maximum rooting depth
$R_{z\text{-min}}$	[m]	Starting depth of seed/plant

Symbol	**Unit**	**Description**
Plant and Root model		
S_r	[m g^{-1}]	Specific root density
t	-	Time
T_{air}	[°C]	Air temperature
T_{max}	[°C]	Maximum temperature for root growth
T_{min}	[°C]	Minimum temperature for root growth
V	[l]	Volume
W	[g m^{-2}]	Standing biomass
W_r	[g m^{-2}]	Root biomass
W_s	[g m^{-2}]	Shoot biomass
z	[m]	Soil depth
z_{max}	[m]	Maximum soil depth
Other		
N	-	Nitrogen
NR	-	Nitrate reductase
NRT1	-	Nitrate transport system gene class 1
NRT2	-	Nitrate transport system gene class 2
NiR	-	Nitrite reductase
GS	-	Glutamine synthetase
GS-GOGAT	-	Glutamate-2-oxoglutarate aminotransferase
LATS	-	Low-affinity transport system
HATS	-	High-affinity transport system
ATP	-	Adenosine tri-phosphate
ADP	-	Adenosine di-phosphate
AMT	-	Ammonium transporter gene
mRNA	-	Messenger Ribonucleic Acid
P_i	-	Phosphate
CO_2	-	Carbon dioxide
AOM	-	Added organic matter
SOM	-	Soil organic matter
SMB	-	Soil microbial biomass

1 Introduction

In intensive arable and vegetable production, crops need a high and balanced supply of nutrients to produce satisfactory yields. Climatic and soil textural conditions have a significant impact on nitrate losses to the surrounding environment. This may cause nitrate concentrations in drinking water to exceed the EU Drinking Water Directive upper limit of 50 mg L^{-1} nitrate (Anonymous 2000). To comply with this Directive, Danish legislation has been implemented in a number of action plans for the aquatic environment, the latest from 2004. Part of these action plans has been to establish regulations for fertiliser application and mandatory use of catch crops to minimise mineral N losses.

Typical catch crops are ryegrasses or cruciferous species, sown before or immediately after harvest of cereals. Under optimal conditions a catch crop can take up 3 to 4 kg N ha^{-1} day^{-1}, contains 3 to 4% N in dry matter and will deplete the soil of mineral N in a few weeks of active growth (Vos & van der Putten 1997). Good catch crop establishment is important for optimal growth and N uptake. Crucifers are more sensitive to date of sowing in autumn than monocot species (Vos & van der Putten 1997; Elers & Hartmann 1987). However, crucifers generally have a higher root penetration rate and rooting depth. This means that crucifers are normally able to reach nitrate in the soil profile before the occurrence of a precipitation surplus and risk of nitrate percolation (Kristensen & Thorup-Kristensen 2004; Thorup-Kristensen 2001).

When designing crop rotations to achieve high N use efficiency, crops should be placed in the crop rotation according to their rooting depth and N demand. At positions in the crop rotation where N leaching losses cannot be prevented in the previous autumn, significant amounts of N can be present at greater soil depths in the spring. Use of crops and catch crops with deep roots strongly improves the possibility to recover N that would otherwise be lost to deeper soil layers and end up in the aquatic environment.

Plant soil models are a valuable tool for improving crop combinations in rotations for optimal use of nitrogen. Plant soil models usually contain different modules for N mineralisation, water movement, SOM, SMB and AOM calculations, and some models have recently been improved in respect of those modules (Abrahamsen & Hansen 2000;

Bruun et al. 2003). However, the modelling of root growth in many plant soil models is simple and with few possibilities to adapt simulated root proliferation and depth distribution to that actually found with different crop species.

Root growth and development is an important issue for better understanding of plant and soil interactions. For optimal yield, roots have to occupy the entire soil matrix where nutrients are located, while to decrease the environmental risk of nutrient losses plant growers have to know where the nutrients are and match them to crop root growth and N demand.

Section 3 describes the soil matrix as a medium for root development and N uptake. The main physical and biological interactions are discussed in terms of root growth, development and N uptake. Section 4 provides a model comparison, where three different SOM sub-modules and two different parameterisations of a crop module are tested to fit a field trial with a crop rotation and nitrate concentration measurements. Furthermore, a model analysis of nitrate leaching and retention with and without the use of catch crops under different soil and climate conditions in Denmark is described. Section 5 focuses on using soil plant models within two different approaches. Modelling of root growth and a new way of using a simple root model for one and two dimensions are discussed.

2 Objectives

The overall aim of this Ph.D. project was to improve the prediction of soil mineral N availability and loss through improved modelling of crop root development.

The specific objective was to develop and test a root module for simulations of N uptake in a crop rotation system designed for high utilisation of mineral N in short-term rotation planning. The focus was on more accurate root modelling compared with field observations in order to improve the prediction of available mineral N in the rooted zone.

The primary objective was to assess simulation model structure and the impact of different sub-modules on soil nitrate concentration predictions. Plant and soil models commonly include different modules for calculation of organic matter turnover, inorganic N and crop growth. Here one field experiment was simulated to test different module settings for nitrate concentration calculations. The question tested was:

- What are the consequences of applying different SOM and crop modules (differing in pool structure or parameterisation) in the soil-plant-atmosphere model *Daisy* on simulated crop production, soil N dynamics and soil nitrate concentrations of a pasture and cereal cropping sequence?

From simulating a single field trial on one site, the next objective was to analyse different modelled root growth of two catch crops in autumn and analyse the effect on nitrate retention in spring in a range of different soil type and climate interactions. In Denmark, the amount of precipitation shows a large variation geographically and annually. Furthermore, the typical soil texture classes vary greatly geographically. Combining different root growth properties with soil texture and climate regimes, the following questions were asked:

- What is the effect of nitrate retention in soils of different textural properties subject to different precipitation regimes, and how much does this vary between years?

- Does the use of catch crops and their rooting depth affect nitrate distribution in the following spring?

- Does the rooting depth of the following main crop affect the decision on whether to use catch crops and if yes, which type of catch crops should be used?

The third objective was to investigate how a sub-module for root growth could be improved. A root module for simulations of N uptake in a crop rotation system designed for high utilisation of mineral N in short-term rotations was developed. The focus was on more accurate root modelling for one- and two-dimensional crops in order to improve the prediction of available mineral N in the rooted zone. Plant models for crop rotation simulation are often used for better utilisation of added and residual N in soil, in order to optimise plant production and minimise the impact on the surrounding environment. Most of the models used for this purpose are only suitable for simulation of monocot crops. The questions tested in this part of the project were:

- Is it possible to develop a simple root model capable of simulating root densities with depth in soil layers for greatly different arable and vegetable crops?

- Can improved simulation of root density with depth be used for more accurate simulation of N uptake from different soil layers?

Before the objectives are discussed in the sections on modelling studies, a review of root development in the soil matrix is presented to introduce abiotic and biological properties in soil. The influence of soil texture and microclimate on root growth and the differences in root growth and development between monocot and dicots are explained using examples from field experiments. Furthermore, the nutrient uptake mechanism of roots is reviewed with particular emphasis on N. Some of the activities occurring in the rhizosphere are important in understanding root growth, root functions and nutrient uptake, but were not directly used in the current simulation studies.

3 Root development in the soil matrix

The primary functions of the root system are anchorage of the plant in the soil and acquisition of soil resources such as water, N and other nutrients. However, roots also serve as storage organs and synthesise growth regulators. Different crop species or genotypes can differ in terms of root penetration rate, rooting depth, root density and biomass. Soil physical factors such as pore size and distribution, root penetration resistance and nutrient and water availability are the main physical factors affecting the root distribution. For optimal plant growth, roots have to supply the crop with water and nutrients. For this purpose, root length, density, diameter, surface area, depth and contact with water play an important role, as these factors can be inhibited or restrict root development into the soil matrix.

The environmental conditions in the soil have to be optimal for full development of a root system. Root growth, development and function are largely determined by genetic information, but respond, often substantially, to availability of carbohydrate supply and local environmental conditions encountered during growth. Soil conditions can affect the extent and morphology of growing root systems directly or indirectly. These include water content, soil strength or mechanical impedance and thermal regime.

3.1 Physical barriers to roots

Size and distribution of soil pores are important for root growth, because air, water, nutrients and roots are located in the pore space of the soil matrix. Figure 3.1 shows a schematic overview of root functions occurring in the rhizosphere. Bulk density and porosity are inversely related, so when bulk density increases total porosity decreases. Variations in bulk density can occur both horizontally and laterally due to changes in texture, structure, organic matter content, biological activity and soil management. There is a relationship between root growth and soil physical stresses, including mechanical impedance, water stress, oxygen deficiency and bulk density (Bengough et al. 2006; Materechera et al. 1991). Singh and Sainju (1998) found that with increasing bulk density, root length decreased and root diameter increased in many seedlings. Well-structured soils have many stable aggregates in a wide range of sizes, which gives a good balance between aeration and water-holding capacity. Well-structured soils often have a

high clay content, which has a lubricating effect when roots penetrate the soil. In structured soil, it has been reported that up to 80% of the roots are placed within the surrounding 1 mm of macropores in soil (Hinsinger et al. 2005). Unstructured soils generally have lower clay content and higher sand and coarse sand content, low or no aggregate content and consist more of a single-grained structure, which has a higher penetration resistance. Madsen (Madsen 1985) investigated 50 soil profiles in sandy soil where maximum rooting depth was 0.70 m and in sandy loam where maximum rooting depth was 1.40 m and concluded that differences in soil texture explained the differences in rooting depth. However soil bulk density and soil structure are not the only factors determining root development. In clayey soils porosity often occurs as cracks, allowing roots to penetrate to deeper soil layers. It is also important for roots to have an adequate supply of oxygen. As a rule of thumb, soil should contain more than 10% air filled pores at field capacity to maintain aeration.

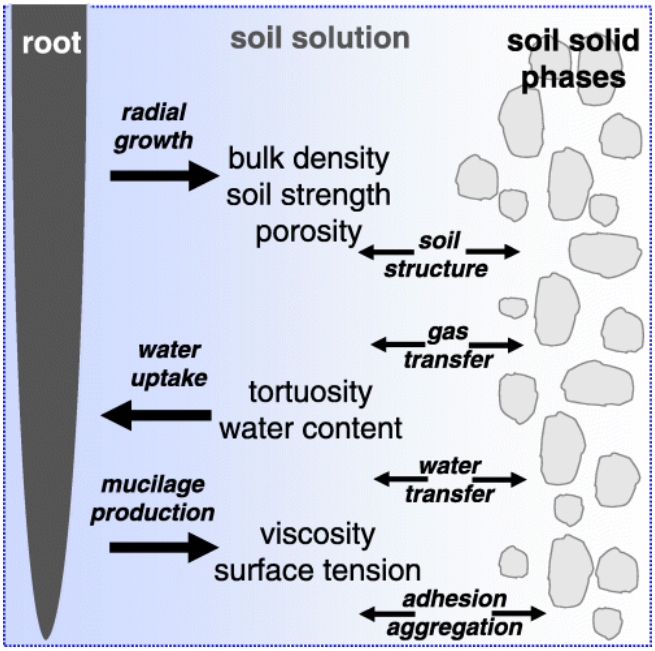

Figure 3.1. Schematic representation of root functions involved in changes in biochemical properties occurring in the rhizosphere. Source Hinsinger et al. (2005).

Organic matter compounds can temporarily bond with quartz and clay and form stable aggregates. Soils containing adequate amounts of organic matter are therefore less prone to compaction and can promote earthworm activity. However, the organic matter is often located in the topsoil layer and is not related to deep rooting growth. Earthworms create new macropores important for aeration, water flow and root passage though compact soil layers. Roots in themselves also create bio-pores, which increase aeration and infiltration

of water and provide pores for succeeding crops (Stirzaker et al. 1996). The presence of roots in the soil matrix may also affect soil structure by supplying organic matter through the release of exudates and decay of old and dead roots. Dead roots can stabilise soil aggregates and increase root-soil hydraulic contact. Root development is generally reduced at low pH. Johnson & Wilkenson (1992) found root length and root fresh weight to be positively correlated with pH in the range 4.0 to 6.0.

Soil temperature effects on plants are both direct and indirect. Temperature affects seed germination and seedling development, root growth and nutrient uptake, nutrient availability and decomposition of plant root residues. Growth increases with temperature until an optimum is reached and then declines if temperature rises further. The optimum for maximal root mass production is highly dependent on plant species, e.g. for oats (*Avena sativa L.*) it is only 5 °C compared with 26 °C for maize (*Zea mays L.*) (Glinski & Lipiec 1990). Primary roots are able to grow over a much broader range of temperature than branch roots. Roots grown at low temperature may be less branched, and temperatures higher than the optimum may reduce elongation rates and increase branching. A secondary effect of high temperature on roots can be that pathogens can more easily infect the stressed root. At low temperatures, water uptake and nutrient uptake by root systems may be reduced. At higher temperatures, the growth rate increases significantly as the available water increases (McMichael & Burke 1998). Root metabolism also becomes more sensitive at high temperatures.

Soil texture has some influence on temperature fluxes in soil. The heat capacity of quartz, clay minerals, water and aerated pore space is important for how fast the soil can be heated in the spring or cooled in the autumn. Sandy loam has more small pores than a sandy soil and therefore it also has a higher field capacity. The amount of water generally present in the soil affects the heat capacity and is therefore important for how fast the temperature increases or decreases. At the time of planting for most summer annual crops, a temperature gradient has developed in the soil profile with temperature decreasing with depth, and in temperate regions expansion of crop root systems is often limited by the cool spring temperature (Kaspar & Bland 1992). In addition, root developmental processes, which control the duration of cells and organs, interact with root growth processes, which control cell elongation, root length and diameter (Kaspar &

Bland 1992). Excessive temperature results in shorter growth duration, shorter cells, shorter root systems and smaller root diameter than under optimal root growth conditions. Root orientation is influenced by temperature through its impact on the direction of root growth. Crop species with the same temperature optimum can differ in their response above and below this temperature. Winter annuals or cereals that are grown in cool climates, such as oats, oilseed rape (*Brassica napus)* and winter wheat (*Triticum aestivum*), show a higher positive response at low temperature than e.g. maize (Kaspar & Bland 1992).

A review by Clark et al. (2003) found that drought can increase soil strength in many soil types, as it increases with decreasing soil water content. A soil water matric potential of 0.1 MPa can have an effect on soil strength although not affecting root elongation directly. Therefore, Clark et al. (2003) concluded that in many drying soils, the effect of soil strength on plant growth is greater than the direct effect of low matric potential. Drought conditions result in deeper root penetration and higher root distribution in the subsoil than in surface soil. (Singh & Sainju 1998) found that exposing maize to 18 days of drought decreased root counts by 37% in the 0-20 cm layer, but increased roots 50-fold in the 60-150 cm layer. However, soil drying increases mechanical resistance and can restrict root growth. Soil strength can increase by an order of magnitude as the soil dries from a matric potential of pF 4 to pF 4.2 (Ley et al. 1989). Depending on the crop species and soil type, a penetrometer resistance of 1.5 MPa can slow down root elongation by 20 to 75%, and this mechanical impedance is often the major limitation to root elongation.

The mechanical strength of a soil protects its pore space from collapse under the overlying weight, but it also impedes root growth. Roots must apply a force greater than the mechanical strength of the soil matrix to elongate. The impedance depends on adhesive and cohesive forces between soil particles, which in turn depend on water content, texture, porosity or bulk density, pore size distribution, organic matter content, aggregate size. Aggregates are often subdivided into micro- and macro-aggregate groups, where Oades and Waters (1991) define micro-aggregates as formed by fine silt and clay particles and small plant debris, their stability deriving from their original organic matter content, but note that some aggregates are void of organic matter due to

decomposition. Macro-aggregates are formed by micro-aggregates and particulate organic matter held together by fine roots and hyphae.

Plant roots and root hairs serve as temporary binding agents between all sizes of aggregates. This may change structure and give new pore space for soil microbes, roots and water and good contact to the soil surface for uptake of nutrients. Aggregates can be disrupted by a variety of mechanisms depending on the nature of the bonding agents. Plants roots have to make an effort to penetrate the aggregated soil matrix. Most species show considerable or complete root growth inhibition in none structural soils and this leads to a reduction in rooting depth. For example, Barraclough & Weir (1988) found root depth of winter wheat decreased from the norm of 1.4 m in a loam sand soil to 1.0 m in a sandy soil.

Some plants species such as alfalfa, cotton and sweet clover have the ability to penetrate compact soil, and when those roots decompose new macropores are created. Hard layers can arise through traffic by heavy machinery or be present as a fragipan, duripan, argillic or alluvial horizons. Such layers can occur at any depth in the soil profile and root growth is dependent on cracks and bio-pores. A shallow watertable can also stop root penetration unless roots can grow in anaerobic conditions, and this limits the volume of the soil matrix available for exploitation by roots.

Tillage can alter soil bulk density, porosity, aggregation and mechanical impedance and therefore affect root systems. Reduced tillage promotes the development and persistence of aggregates, structural voids and bio-pores in the zone of highest root activity (Wraith & Wright 1998). However, reduced tillage can also have a negative effect on arable land, because it can create pathways for preferential flow, so that water from precipitation or irrigation bypasses the root-containing layer. Mechanical impedance is increased by compaction or decreasing water content, the latter through its effects on increased inter-particulate cohesion, particularly in soils with high clay content. There is a commonly reported near-linear decrease in root penetration with increasing mechanical impedance (Wraith & Wright 1998).

Water uptake by roots can result in dry soil layers below the rooting front and this restricts the maximum rooting depth. The interaction between the soil strength

characteristic, the soil water balance and the evapotranspiration rate determines whether mechanical impedance limits root growth (Bengough 1997). Increasing soil water content may decrease mechanical impedance, rate of gas diffusion or soil nutrient availability, and modify the soil temperature regime (Wraith & Wright 1998). Favourable soil structure and high aggregate stability are important for soil fertility and enhancing porosity and tend to increase root length density. As the soil dries out, the water becomes less available and the soil becomes harder for roots to penetrate. The effect of soil strength often depends more on soil texture than water content. Coarse or silty soils seem to have higher soil strength and lower water content than loamy and clayey soils. Compaction increases bulk density and highly increases soil strength, which results in impeded root development.

3.2 Shape and form of root system architecture

After germination of the seed or transplanting of a plant, roots begin to develop vertically and horizontally. The root system starts with a primary root system that is always mono-axial. These primary roots develop lateral roots called first order roots (see Figure 3.2) that are nearly all fibrous and that are always present on young primary roots but do not all persist as the root ages (Cannon 1949). The first order roots again have branches called second order roots and so forth. Adventitious roots can develop from the stem and these can subsequently develop lateral roots. Adventitious roots often have additional functions to nutrient uptake such as anchorage, see Figure 3.2 (Cannon 1949)TT.

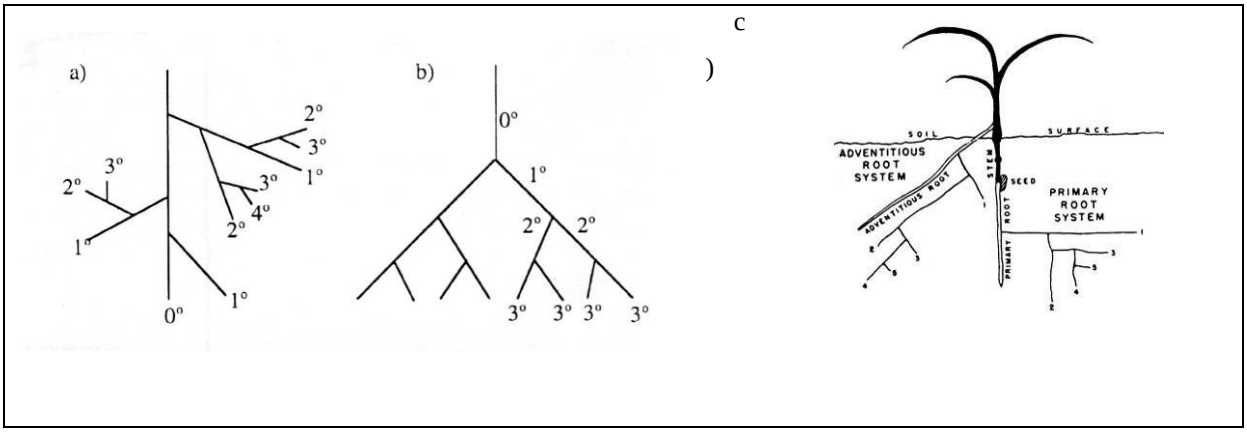

Figure 3.2. a) dicot root system with taproot; b) bifurcated dicot root system; c) monocot (maize) root system. Numbers indicate order of branching. Sources: a and b Dunbabin (2003), c Cannon (1949).

The primary root is usually positively geotrophic, although the depth and architecture differ greatly between crop species. Figure 3.3 shows different examples of root systems.

Type 1 (maize) is typical of monocot crops. Types 2 and 3 are typical root systems for dicots and common systems for arable crops. Root architecture can be defined based on some characteristics such as the distribution of branches, the length and diameter of internodes and two angles of branching (Fitter & Stickland 1991; Fitter et al. 1991). Root systems can have a herringbone morphology where branches only originate from the main root axis or can be more complex with more branches and internodes. A more branched root system can be an advantage in acquisition of soil nutrients (Fitter & Stickland 1991).

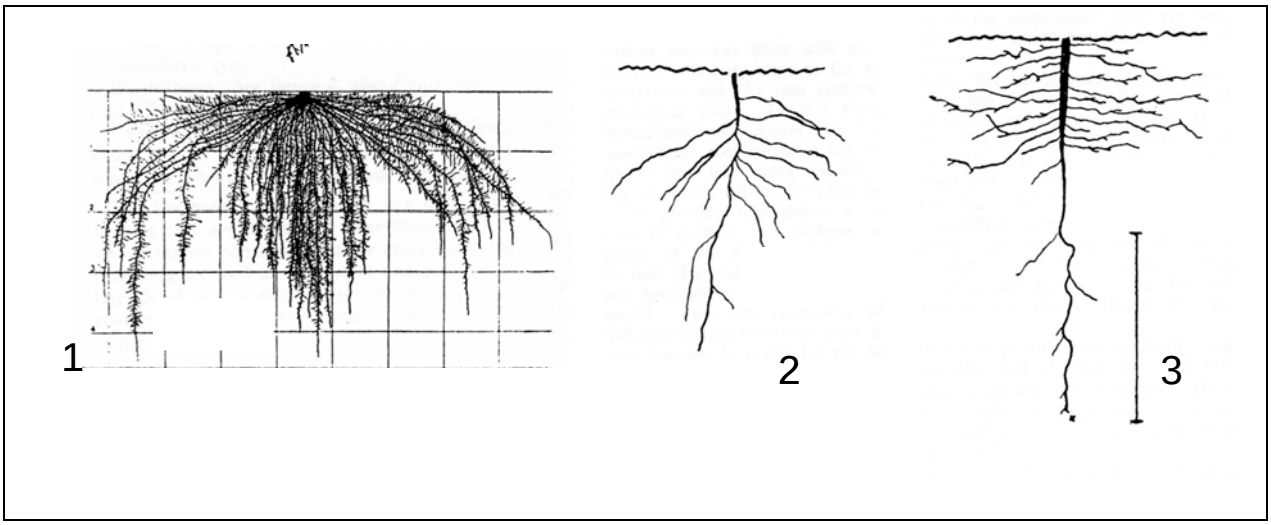

Figure 3.3. Primary root systems for 1) monocot, 2, 3) dicot. Source: (Cannon 1949).

Monocot plants include grasses and cereals. Monocot roots start growing from the embryo on the hypocotyl, then adventitiously or as a node from the meristem at the end of the stem base. After adventitious roots begin to grow the initial primary root dies off and a crown root system is developed. The new roots generally grow to produce tillers and are composed of a cortex of variable thickness surrounding a central stele with vascular tissues. The crown roots of wheat grow outwards at an angle for some time before turning downwards, which is typical of monocot root systems (Rickman et al. 1995). The root system of monocots is exponentially distributed, with many lateral branches in the upper part of the soil profile and fewer branches in lower parts (Gerwitz & Page 1974; Barraclough & Leigh 1984).

The root system morphology of dicots varies widely within this plant group. Roots are initiated at the root apical meristem and produce a taproot with lateral branches as shown in Figure 3.3 (parts 2 and 3). In many plants the taproot may comprise more than the half

the belowground biomass, and it serves as a storage organ in biennial crops. In contrast to monocot roots, dicot roots can have secondary growth that starts from the vascular cambium, and therefore different dicots can have a large variation in root diameter. Dicots often have a greater proportion of roots in the subsoil, whereas monocots tend to have a large proportion in the topsoil.

Root growth rate depends on soil temperature and is often linearly correlated to day-degrees at different base temperatures. In models, root penetration rate r [mm day^{-1}] is calculated for instance using a base temperature of 0 ˚C for cereals and 10 ˚C for maize (Barraclough 1984). Barraclough & Weir (1988) found root growth rate for winter wheat to be 12 mm day^{-1} during autumn, 5 mm day^{-1} during winter and 18 mm day^{-1} during spring. As mentioned in sub-section 3.1, root penetration rate can also be affected by soil texture and compaction. An important parameter of root growth is root penetration depth, but for more detailed research estimated values of root length and density are also needed. Root length increases exponentially with time during the first weeks of seedling growth and increases linearly until the plant changes from the vegetative to the reproductive phase.

Root density can be determined quantitatively by taking soil samples in cores with a given volume and depth and then washing the roots out from the soil. Root length can then be determined by the line-intersect method, where intersects of roots with straight lines (with a given length, on a given area) are counted (Tennant 1975; Newmann 1966).

Another method involves inserting diagonally into the soil a clear acrylic tube, also called a minirhizotron (see Figure 3.4), where the amounts of roots on the upper surface of the tube are filmed. The upper part of the tube contains a 40 mm x 40 mm grid and if the tube is inserted 30° from the vertical, each grid square represents a 34.5 mm soil layer. Minirhizotrons provide three measurements, root depth, root frequency (percentage of 40x40 mm^2 gird sections where roots are observed within a given soil layer) and root intensity (the total number of roots crossing the line in each 40x40 mm^2 grid section, with values given as root intersection per metre line).

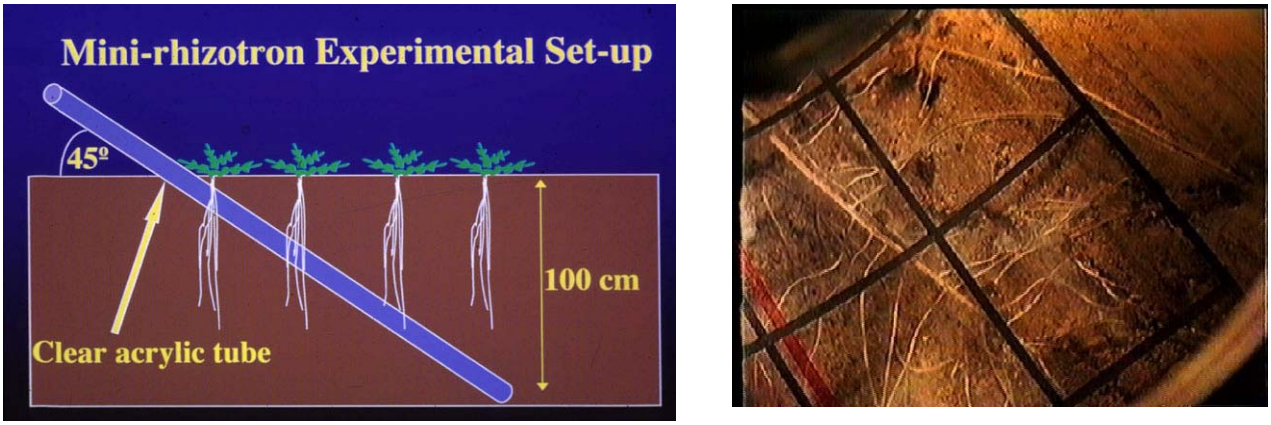

Figure 3.4. Left: Diagram showing use of a minirhizotron. By using a video probe within the minirhizotron tube, it is possible to get information about penetration rate, rooting depth, root frequency in and between rows and at different depths (DiTomaso 2001). Right: Minirhizotron image of oil radish roots (*Raphanus sativus oleiformis*) (Source: Dept. of Horticulture, Faculty of Agricultural Sciences, University of Aarhus).

Measurement of root intensity can be comparable with root length density measurement by the soil core technique (Merrill & Upchurch 1994; Samson & Sinclair 1994; Buckland et al. 1993). The minirhizotron technique is also less time-consuming than the soil core method. However minirhizotron have an appreciable error in root estimation in the upper soil layer (0-0.1 m) (Ephrath et al. 1999; Heeraman & Juma 1993).

On a global scale, distribution of root biomass, and thus root length, is about 45% in the soil layer 0-0.1 m, 50% in the soil layer 0-0.2 m and 75% in the soil layer 0-0.4 at latitude 80°, the root biomass near surface increases to latitude 30°. Root biomass is positively correlated with annual precipitation and length of warm season and only weakly correlated with climate (Schenk & Jackson 2002). In an experiment comparing monocots and dicots as catch crops, Thorup-Kristensen (2001) showed that monocot root density is high in the plough layer but is low at depth both early and late in the season, as shown in Figure 3.5a, b. Figure 3.5 also shows values for three dicotyledon crops, which after 6 weeks showed the same pattern as monocots but after 3 months had a much higher root density deeper in the soil profile. Root frequency is an indirect indication of root density in different soil layers. Figure 3.5c shows a high frequency for both monocot and dicot crop species in the upper soil layer, but in deeper layers root frequency for monocots declines while dicots maintain a high frequency. Gregory (2006) found the same distribution for winter wheat but also cauliflower, with high root length density in the top layer but decreasing value in deeper layers (Figure 3.6). A reason for this could be the short growth period cauliflower had from transplanting to harvest. Rape

and sugar beet (Figure 3.6a) show the same trend as other dicots (Figure 3.5a,b,c), with high root density in the whole soil profile.

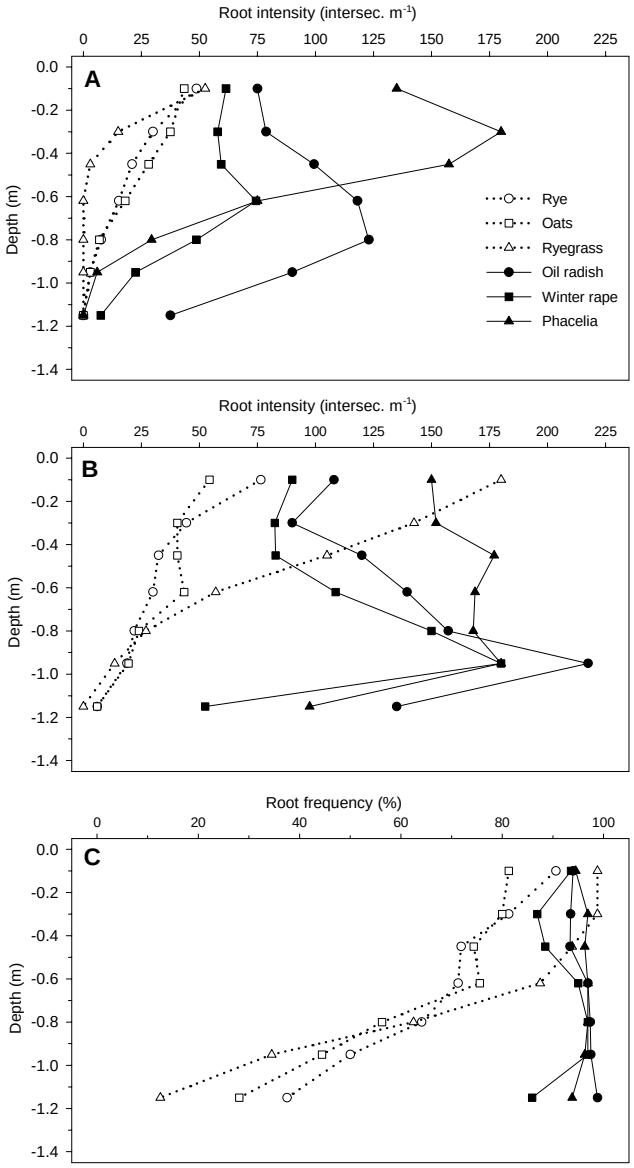

Figure 3.5. Root intensity (a) 6 weeks after sowing (late July) and (b) in November; (c) Root frequency in November. Solid lines = dicot crops, dotted lines = monocots, for plant species see key in (a). Source: Modified after Thorup-Kristiansen (2001).

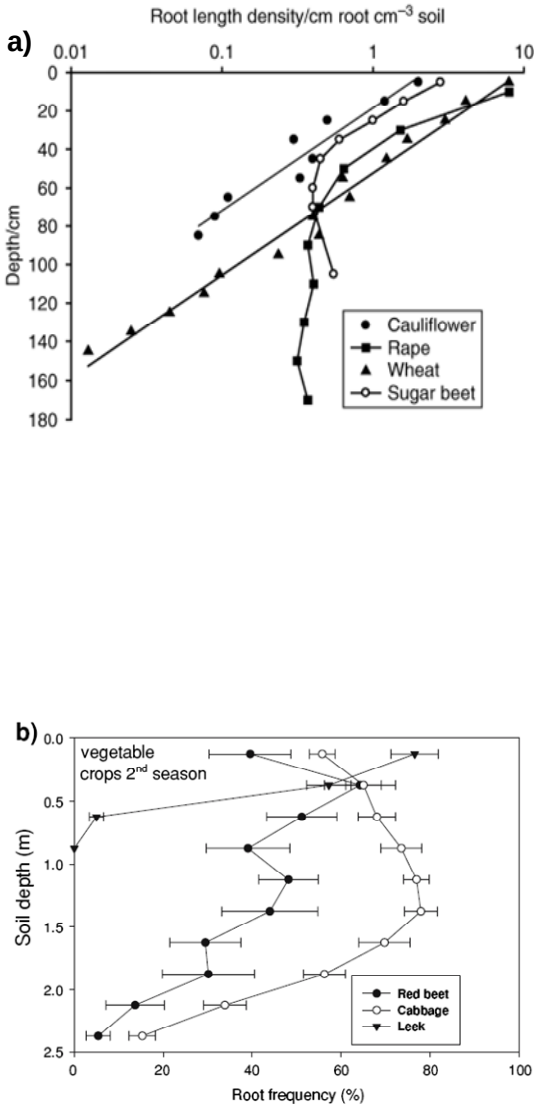

Figure 3.6. Distribution of roots with depth in the soil profile for maturing crops. a) Root density of cauliflower, oilseed rape, winter wheat and sugar beet. b) Root frequency of red beet, cabbage and leek. For crop species see key in diagrams. Sources: a Gregory (2006), b Thorup-Kristiansen (2006).

3.3 Root length and distribution

The ability of a genotype to express different responses to the physical environment is termed phenotypic plasticity. Root growth and distribution can vary significantly

between cereal cultivars, and can be important for farmers with respect to maximising crop yield (Marschner 1998). The depth and proliferation of roots in response to seasonal variations in precipitation and to soil texture are some of the reported responses (Jordan & Miller 1980; Jordan & Monk 1982). In years with high precipitation, shallower rooting depth than in years with low precipitation has been reported. Another manifestation of phenotypic plasticity is the change in length and density of root hairs in response to availability of phosphorus. Spring barley and winter wheat show different growth of root hairs, which has a great effect on uptake of immobile nutrient ions such as phosphate-P (Gahoonia et al. 1997; Gahoonia & Nielsen 2004). Williamson et al. (2001) showed that low phosphate availability in soil favoured root growth through increasing lateral root length and density, while Nacry et al. (2005) showed that auxin seemed to control the changes in the root architecture.

3.4 Root uptake of nutrients

Plants require the 16 essential elements C, H, O, N, P, K, Ca, Mg, S, Fe, Cl, B, Mn, Mo, Cu and Zn and some species also require other elements such as Ni, Si, Co and Na (Marschner 1995). For plants growing in soil these elements are mainly obtained (except C and O) from the soil through the roots. Roots extend into the soil matrix to acquire nutrients and almost all nutrients absorbed by plants are in inorganic form. Roots are selective in ion uptake and therefore certain nutrients are taken up preferentially, while others are discriminated against or excluded from uptake. Root cells can accumulate much higher concentrations than are present in the external solution.

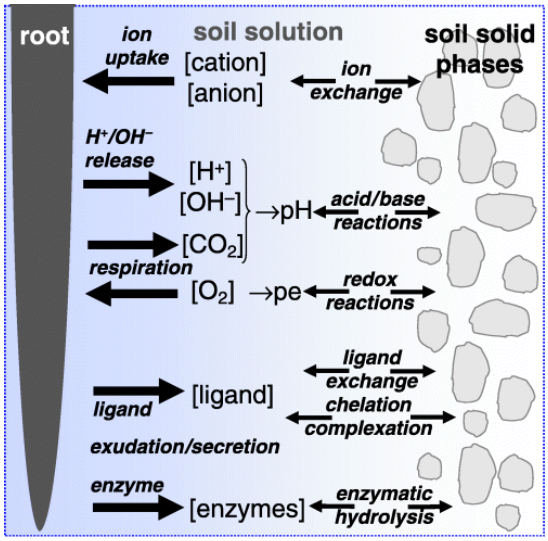

Figure 3.7. Schematic overview of root functions involved in changes in physical properties in the

rhizosphere for optimal nutrient uptake. Source: Gregory & Hinsinger (1999).

The acquisition efficiency of the root system can be described as the soil volume and water-filled pore space with which the roots and root hairs come into contact. Figure 3.7 shows a schematic overview of root processes involved in determining the physical conditions for optimal ion uptake, but these processes can be highly different between plant species and genotypes. There are three basic pathways of nutrient uptake (Marschner 1995):

- Root interception: When roots penetrate the soil matrix they occupy new volume and additional nutrients become available. In general, root volume in the topsoil layer is 1% of the total volume and only a small part of the total nutrient uptake comes from interception. As shown in Table 3.1, root interception is mostly of importance for Ca and Mg uptake. Mycorrhizae can increase nutrient uptake by root interception through the surface area and soil volume that these mycorrhizae occupy. This mechanism can be important for P uptake in some crop species.

- Mass flow: This is transport of bulk soil solution along the water potential gradient driven by the respiration of the plant. The main factors here are nutrient concentration in the soil solution and amount of water transpired. Table 3.1 gives estimated values for mass flow uptake. Mass flow is important for mobile ions such as nitrite and sulphate, whereas immobile ions are highly affected by sorption/desorption processes and therefore have a low concentration in the soil solution.

- Diffusion: Uptake by diffusion is driven by transport along a concentration gradient. Typical plant requirements of K and P are supplied by diffusion as shown in Table 3.1. When plants deplete the zone near the root surface of ions, other ions from places with higher concentrations diffuse towards the lower concentration and enter the root zone.

Water content in the soil is highly determining for the diffusion rate. Jungk (1991) noted in a review that nitrate and K diffusion in water is two or more orders of magnitude faster than in porous and aerated soils. When ion concentration is changed by plant

uptake, ions can be released by desorption from the surface of mineral and organic compounds and become available for uptake close to the root.

Table 3.1. Estimated nutrient supply from the soil by root interception, mass flow and diffusion in maize roots for production of 9500 kg cereal grain ha^{-1} (Barber 1984).

		Supplied by (%)		
Nutrient	**(kg ha^{-1})**	**Interception**	**Mass flow**	**Diffusion**
Nitrogen	190	1	79	20
Potassium	195	2	18	80
Phosphorus	40	2	5	93
Magnesium	45	33	222	0
Calcium	40	150	375	0
Sulphur	22	5	295	0

3.4.1 Ion absorption by the root

Transport between membranes can be driven passively by a gradient from higher to lower concentration. As the concentration of most macronutrients in the plant solution is higher than that in the soil solution, their uptake may require an ion-specific uptake mechanism where energy, provided by respiration, is expended. Membrane transport against concentration gradient is linked to an energy-consuming mechanism which takes place in proton and redox pumps. Pumps are located in both plasma membrane and tonoplast, and their primary function is the regulation of the pH in the cytoplasm. Cations are transported along the electrical potential gradient across the plasma membrane into cytoplasm in a uniport at high concentrations in soil solution. At low concentration energy is needed in a proton symport transport. Anions are transported in plasma membrane as a proton/anion cotransport, while in tonoplast transport is linked to proton pumps. Energy demand for ion uptake can consume as much as 35% of the total respiratory energy of the plant (Marschner 1995).

There can be a passive transport of nutrients in the free space in roots and this is kinetically controlled by diffusion and mass flow. Ion exchange occurs between the solution and the negatively charged cell walls. The ion diffusion across an area with a constant concentration over time is given by Fick´s first law, while Fick´s second law can be used to determine diffusion with non-steady state concentration over time. Equation 1 shows the change in concentration over time:

$$\frac{dC}{dt} = \frac{1}{r}\frac{d}{dr}\left(rD_s \frac{dC}{dr} + \frac{r_o VC}{b} \right) \qquad \text{Equation 1}$$

where C = concentration in soil solution, t = time, r = radial distance, r_o = root radius, V = volume and b = buffer power of the soil. Active transport mechanisms move specific ions into the cytoplast across the plasmalemma and vacuole across the tonoplast. Ion channels can be cation- and anion-selective; they transport ions inward or outward, at ion fluxes that are orders of magnitude larger than those through ion carriers. Carriers bind the specific ion and move it across the membrane and subsequently release it. Active nutrient uptake can be up to 10 orders of magnitude larger than simple diffusion and active uptake can reduce the average nutrient concentration in the soil water solution, whereas passive uptake does not alter ion concentration.

Sanders et al. (1984) developed an algebraic model of ion transport kinetics across membranes including concentration and concentration gradients of carriers on substrate transport. To describe ion-specific enzyme-catalysed reactions, Sanders et al. used Michaelis-Menten kinetics with the parameters K_m and J_{max}. Uptake of a single ion J^* is (Equation 2):

$$J^* = \frac{J^*_{\max}\left(c - c_{\min}\right)}{K_m + \left(c - c_{\min}\right)}, \qquad \text{Equation 2}$$

where $J^*_{\max}$ is the maximum uptake rate (uptake per unit length of root) and K_m is the Michaelis constant. K_m magnitude is inversely related to binding energy between substrate and enzyme, and denotes the concentration where J^*=0.5 $J^*_{\max}$. A graphic overview of equation 2 is shown in Figure 3.8, where C_{min} is the concentration where influx becomes operational. The dimensions of J^* can be (mass of nutrient / biomass of root) or (mass of nutrient / root surface area). K_m varies between plant species, plant age, nutrient type and nutritional status of the plant.

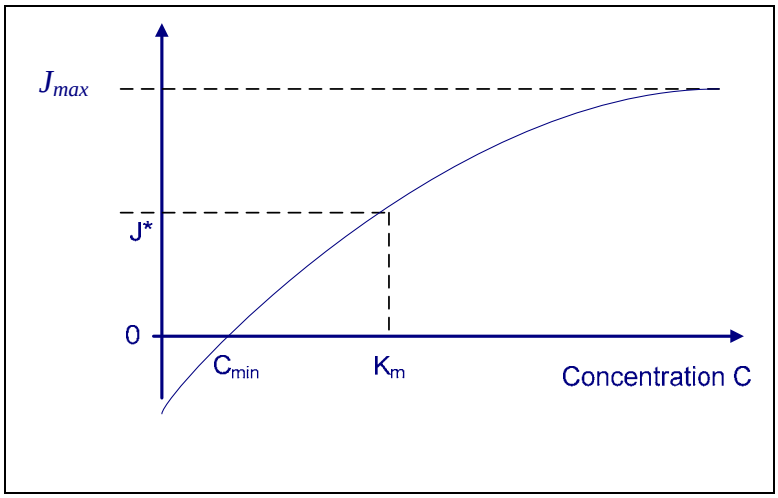

Figure 3.8. Characteristics for Michaelis-Menten description of active nutrient uptake by plant roots.

Herringbone root systems show low overlapping and can be efficient for acquisition of mobile nutrients, whereas dichotomous root systems represent a superior system for uptake of both mobile and immobile ions because of the more branched architecture (Fitter & Stickland 1991). With higher root density the diffusion distance of ion uptake is shorter. Nitrate can move about 10 to 100 mm day^{-1} in soil, where phosphorous ions only diffuse within 0.01 mm day^{-1} of a root surface. Nitrate diffuses approximately 10-fold faster than ammonium, which influences the uptake ratio of the two ions (Clarke & Barley 1968). Considering the whole root system as a summation of each single root and uptake of nutrients from the soil cylinder around each root, this soil volume decreases as root length increases. Furthermore, root architecture is important as dispersal of roots minimises competition between roots within the root system. This is termed exploitation efficiency (Fitter et al. 1991). When roots are placed close to each other, they have overlapping depletion zones and this decreases the exploitation efficiency. Acquisition of phosphorous is particularly efficient when the roots are regularly distributed in the soil, whereas inter-root competition is higher for more mobile ions such as nitrate.

The assumption that the soil cylinder around the root can be used to model nutrient uptake was shown by Baldwin (1975), who reported good accuracy for rape as the model crop. However Brewster et al. (1976) showed that the soil cylinder assumption underestimated P uptake in rape because rape acidifies the rhizosphere, which increases the soluble concentration of P, and this reaction is not considered in the model. Furthermore, Robinson et al. (1991) found that the model overestimated nitrate uptake from both fertilised and non-fertilised experiments. This assumption of the root system

as geometrically uniform is thus not valid. Under some conditions a number of roots may grow into a clump in pre-existing pores or earthworm channels, where root length can be high, but only search for nutrients as one root with a large diameter and hence only utilise a small part of the soil volume.

Nitrogen uptake

Plant uptake of nitrate or ammonium as a sole N source depends on many factors. In general, *calcifuges* (plants adapted to acid soils and low redox potential) prefer ammonium and *calcicoles* (plants adapted to calcareous soils) prefer nitrate. However, the highest growth rates for most plant species are obtained with a combination of both. The form of N supply has a strong impact on uptake of other cations and anions and on pH in cell and rhizosphere.

Nitrate is taken up by active transport across the plasma membrane with a cation co-transport or counter transport process via carriers. It is dependent on ATP supply to the H^+ ATPase and ends up with a pH increase in the rhizosphere, as shown in Figure 3.9 (Miller & Smith 1996; McClure et al. 1990). Depending on external nitrate concentration, both high- and low-affinity uptake systems can be found. One study generally found two high-affinity systems (HATS) for nitrate concentrations below 0.5 mM and one low-affinity (LATS) above this concentration (Glass & Siddiqi 1995). Two gene families, *NRT1* and *NRT2*, have been identified from the high numbers of nitrate transporter genes (Crawford & Glass 1998). It was first believed that *NRT1* mediated the LATS system and *NRT2* the HATS system (Forde & Clarkson 1999), but Liu et al. (1999) found that the low affinity transporter gene (*AtNRT*1.1) also functions in the high affinity range in *Arabidopsis*.

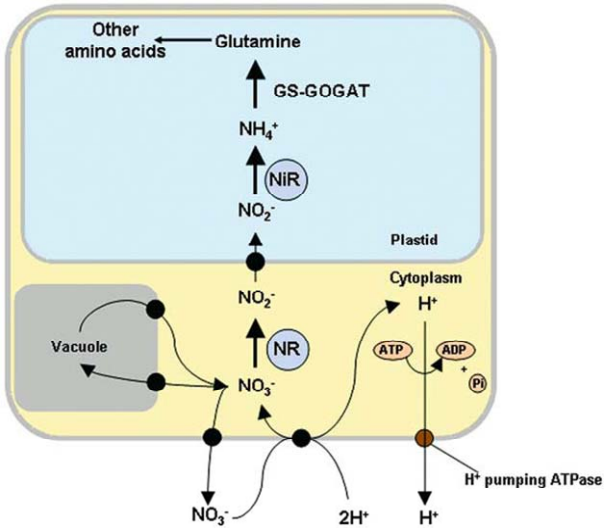

Figure 3.9. Nitrate uptake in roots and assimilation in plant cells. Source: Miller and Cramer (2005).

A molecule of ammonium is assimilated by excretion of one proton and hence decreases rhizosphere pH (Ayling 1993). Similarly to nitrate, a range of ammonium transporter genes (AMT) have been found and, as for nitrate, some of these are expressed in root hairs and contribute to ammonium uptake (Ludewig et al. 2002).

Preferential uptake of ammonium or nitrate has been reported under different conditions. For instance MacDuff & Wild (1989) examined interactions between N deficiency and preferential uptake of ammonium and nitrate by oilseed rape under hydroponic conditions. They reported that plants growing for 7 days under N starvation had an ammonium to nitrate uptake ratio of 0.4-0.6, compared with 0.6-0.8 in plants grown with a continuous supply of N. Nitrate and ammonium could be expected to have a mutual influence on each other since both are metabolised through the same pathways in the root after nitrate is reduced to ammonium. However ammonium has been shown to be preferable for most plants and high ammonium concentrations can have a negative effect on nitrate uptake (Barber 1984; Taylor & Bloom 1998), whereas high nitrate concentrations in soils have no effect on ammonium uptake rate. Bloom et al. (2006) reported a similar reaction in young roots of maize.

The presence of ammonium stimulates root elongation and accumulation of biomass in the root apex, and reflects the fact that assimilation of one ammonium to glutamine only consumes 2 ATP equivalents, whereas assimilation of one nitrate ion consumes 12 ATP equivalents.

Net uptake of nitrate is regulated by plant demand and signals from the shoot are transported as amino acids in the phloem to the roots (Tillard et al. 1998). Experiments using ^{15}N and ion-selective microelectrode techniques have shown that high nitrate and ammonium uptake develops just behind the root meristem (Taylor et al. 1990; Henriksen et al. 1990; Lazof et al. 1992). Nazoa et al. (2003) found also a higher uptake behind the root tip in *Arabidopsis*, but found only a 2- to 3-fold increase and concluded that mature parts of the roots still have a high N uptake.

In addition to mineral N uptake, roots are able to take up organic N compounds, mostly as amino acids. Amino acids have a low diffusion coefficient and the effective diffusion in soil is less than 1 mm day^{-1}, 10-fold less for glutamate and 100-fold less for lysine and glycine compared with nitrate (Owen & Jones 2001). Amino acids have a half-life of about four hours in soil and plant roots have to compete with microorganisms, therefore uptake of amino acids tends to be low (Owen & Jones 2001). However it is evident that roots in general are able to take up amino acids and these may be directly incorporated into proteins (Miller & Schmidt 1965), as has been shown *in situ* in forest species (Persson & Nasholm 2001). In experiments with lettuce and squash, where the N supply comprised inorganic N and extract of clover or alfalfa, plant N accumulation was shown to be affected by the total amount of added N and the form of N fertiliser (El-Naggar et al. 2007).

Legumes can be supplied with N by symbiosis with nitrogen fixing endosymbiotic rhizobial bacteria (Vance 2002). Nitrogen gas is fixed and the plant obtains ammonium and N from the atmosphere when inorganic N is limited in the soil. Legume crops are important in bringing nitrogen into crop rotations where external N fertiliser is too expensive not permitted, as in organic agriculture. Furthermore, plants can be supplied with N though mycorrhizae, although this is associated with P interception. Mycorrhizae increase the potential of roots for extended acquisition though uptake of ammonium and organic N due to the slow diffusion of those two compounds and due to active uptake of organic N (Buscot et al. 2000).

3.4.2 Root density and nitrogen uptake

Little is known about the role of root architecture and root density in the acquisition of soil N by plants (Dunbabin et al. 2003). As a mobile ion, nitrate is normally carried along by mass flow and diffusion with the water to the roots, so root growth rate, penetration depth and distribution are of primary importance for nitrate uptake. However the relationship between root density and uptake rate is not linear. When root density is high the uptake rate levels off, caused by overlapping of the depletion zones of individual roots and reflecting competition between roots, and only a small proportion of the total amount of roots may be effective in N uptake (Robinson 2001).

Soil physical conditions may also have an effect on N uptake. In places with low root densities, decreasing water content means that a smaller proportion of pores are water-filled, this greatly limits diffusion of nitrate to roots. This has often not been taken into account, because most experiments are carried out in appropriately moist and well-structured soils (Kage 1997), so the subject is not well understood.

For a cash crop in an arable system, N is often added on the surface or in the surface layer, optimally synchronised with the plant N demand and near roots in the surface layer, where all crops have sufficient root density for N uptake. In some organic crop rotations or systems with low fertiliser inputs, the availability of N can be low and depends on decomposition of organic matter N. Here N can be placed more heterogeneously down in the soil profile. Furthermore, plants can be used as N catch crops to reduce nitrate leaching losses (Thorup-Kristensen et al. 2003). To ensure a high yield from crops not receiving artificial N fertiliser, it is important to have a deep root system with high density which has the ability to search the whole soil matrix for N. Dunbabin et al. (2003) tested these conditions for a sandy soil with heavy rainfall events and different lupine species with different root densities in the lower part of the root zone and found that one lupine species with a fine root system acquired 30% more N than other species with lower root densities. This shows that root density also has an effect on mobile ion uptake when soil water moves the nitrate downwards in the soil profile (Gastal & LeMaira 2002).

The role of fine roots in nutrient uptake is debated in the literature (Pierret et al. 2005; Zobel 2003; Pregitzer 2002). The quantity of fine roots often dominates the overall root length of the root system, but authors still demonstrate a lack of knowledge about the dimensional, functional and physiological definitions of fine roots, not least whether fine roots die off. With conventional methodology the amount of fine roots is often underestimated because of their size and transparency. Therefore plant root systems could be much longer and probably include more biomass than is generally accepted when using well-known standard values (Pierret et al. 2005). Improvement of techniques for detecting root density at depth and actual rooting depth of roots is one of the important challenges in providing a better basis to model root development and nutrient uptake.

The heterogeneity of N concentration in the soil profile is caused by interactions between climate, vegetation, biological activity and artificial N fertilisation by the farmer. In arable soil, plants often respond with higher root density in patches or zones enriched with nutrients (Robinson et al. 1994). Figure 3.10 shows the response of barley in terms of primary and secondary lateral root production to localised placement of nitrate and ammonium.

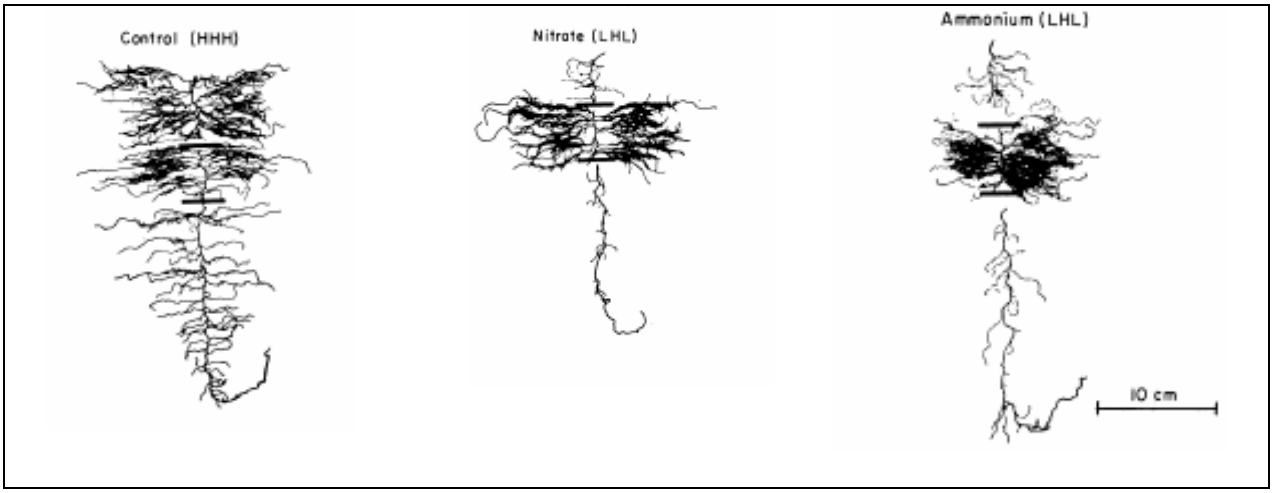

Figure 3.10. Production of primary and secondary lateral roots by barley grown in a hydroponic system. Roots were exposed to 100-fold greater concentration of nitrate or ammonium in the section marked with horizontal black bars, while the control had a high concentration of nutrients in whole root zone. Source: Drew (1975).

This ability to initiate root growth in areas with a high nutrient content can be important for crops competing for nutrients and water. Roots distributed non-uniformly in soil have different access to N, so the plant response to N levels must be coordinated within the

plant, to avoid root development in localised zones with low N when root development is required in other areas with higher N content.

Forde (2002) reviewed the literature for response systems that regulate such plant responses for nitrate uptake and found two regulation mechanisms, local and long-range regulation.

The local response is driven by the cellular ion concentration and seems to be initiated by a threshold concentration. Ion concentration above this threshold modifies regulatory genes controlling the rates of ion transport, and growth and development of lateral roots around the cells (Forde 2002). In hydroponic systems, Granato & Raper (1989) showed that maize root systems increase in density by growth of lateral branches, which supports the theory that local increases in nitrate content can stimulate root branching to get a higher uptake. This is supported by Bloom et al. (2006), who found root growth rate in maize to be increased by adding nitrate or ammonium at the root apex. Even concentration levels as low as 1 mM nitrate can stimulate lateral root proliferation in *Arabidopsis*, but without affecting lateral root initiation as shown in monocots (Zhang et al. 1999). This local response can theoretically happen in every root cell and to avoid it, every cell operates independently by a systemic response system controlled by auxin, as has been demonstrated in *Arabidopsis* via an *ANR1* gene, which is a member of the MADS box family of transcription factors (Zhang & Forde 1998; Walch-Liu et al. 2006).

It is unclear precisely where in the plant the demand-induced signal is generated. Some suggest that the concentration of phloem-translocated amino acids represents the shoot to root carrier of N demand, but Tillard et al. (1998) and others found amino acid concentration to be similar in roots of a N-starved and a N-rich plant. One possibility could be systemic transport of mRNA-based information to send a signal to roots and trigger the development of roots (Citovsky & Zambryski 2000). However, this response does not necessarily occur in all cases with nitrate enrichment, as many studies have found that root density remains the same after enrichment. This agrees with the solute transport theory, where nitrate uptake has a weak association with root density (Robinson 1996).

Other studies report the opposite reaction to the stimulatory effect, i.e. that high N concentration reduces allocation of resources to the roots, decreases root/shoot ratio and reduces root proliferation, and claim that the local root proliferation response is more critical for competition between plants (Hodge et al. 1999). Zhang & Forde (2000) also reported that high nitrate concentration in the whole rooted zone inhibited root length, but not the main root development in *Arabidopsis* in experiments on germinating plants. They concluded that this constituted systematic inhibition related to the amount absorbed.

4 Simulation models as a tool for predicting crop production and environmental impact

4.1 Models for predicting soil organic matter turnover

Models of SOM turnover have often been developed in order to predict crop fertiliser demand or to analyse the environmental impacts of different agricultural management systems. Much of the work on these models has focused on the appropriateness of the basic pool structure of soil organic matter, pioneered by the now classical five-compartment model of Jenkinson & Rayner (1977) which is the early version of RothC, the latest of which is RothC26.3 (Coleman et al. 1997). The RothC26.3 model is an isolated soil organic matter model and simulates the turnover of organic carbon in non-waterlogged soils and can be affected by soil type, temperature, moisture content and plant cover on the turnover process. The model has monthly time steps to calculate total organic carbon. The Sundial model is also a isolated soil model with one pool for decomposition of plant and animal debris and multiple pools for decomposition of the organic matter (Bradbury et al. 1993; Smith et al. 1996). The CENTURY model simulates the long-term dynamics of C, N, P, and S for the whole plant-soil system and is similar to RothC, with a five-pool SOM model (Parton et al. 1987). The model uses monthly time steps and is able to simulate up to several thousand years. *Daisy* is a soil, plant and atmosphere simulation model (Hansen et al. 1990; Hansen et al. 1991), and there is also an updated implementation of the model and a updated calibration of the initialisation of the SOM modules (Abrahamsen & Hansen 2000; Bruun et al. 2003). In the *Daisy* model C and N are divided into three different types of organic matter, AOM,

SMB and native soil organic matter SOM, and it is also possible to place a part of the C and N in an inert pool. The model is based on C pools and calculates the N pools by N/C ratio nitrogen dynamics, calculates turnover of organic matter based on first order kinetics and manages processes such as mineralisation/immobilisation, nitrification, denitrification, nitrogen uptake by plants, nitrogen transport (convection-dispersion equation) and leaching. Recently a new isolated SOM model, CN-SIM, was developed using a comprehensive database consisting of both short- and long-term experimental data (Petersen et al. 2005a; Petersen et al. 2005b).

The CN-SIM model has a structure with two AOM and SMB pools, one SMR (Soil Microbial Residue) pool, one NOM (soil organic matter) pool and one inert pool. The CN-SIM model is included in the soil, plant atmosphere model FASSET (Berntsen et al. 2003). The interface and setup structure of the *Daisy* model allows the user to change the composition of parameters and pool structure and gives the opportunities to build in the CN-SIM module. This opportunity is used in Paper I to compare SOM and crop sub-modules in the *Daisy* model.

4.2 Modules of soil organic matter pools versus modules of crops in models

The objective of Paper I was to analyse the effects of applying different SOM and crop modules (differing in pool structure or parameterisation) in the soil-plant-atmosphere model *Daisy* on simulated crop production, soil nitrogen dynamics and soil nitrate concentrations of a pasture and cereal cropping sequence.

We addressed the following two hypotheses in Paper I: i) Crop production, N assimilation and soil nitrate concentration following a large organic matter input are more appropriately simulated when a more dynamic SOM module is applied; and ii) simulation of the temporal pattern of soil nitrate concentration is affected more by choice of crop module parameterisation than choice of SOM module.

We used an extensive 6-year field experiment for comparing simulated and measured data (Eriksen 2001). The experiment comprised 3 years with perennial ryegrass and grass-clover pastures under different management regimes, followed by cropping with spring cereals (including catch crops) with different application levels of cattle slurry for 3 years.

For simulations of the rotation and SOM and crop module testing we used the plant, soil and atmosphere model *Daisy*. The *Daisy* sub-model for simulating SOM turnover is described in (Hansen et al. 1991) and (Abrahamsen & Hansen 2000). This also utilises the general structure, and in *Daisy* each of these SOM fractions has been divided into two sub-pools; one with a faster and the other with a slower turnover rate. In some models, part of the organic matter may be allocated to a biologically inert pool ('SOM3' in *Daisy*) (Figure 1 in Paper I). Recently, comprehensive SOM pool structure analysis and parameter calibration were carried out on a very large, composite dataset comprising both short-term studies and long-term field experiments (Petersen et al. 2005a; Petersen et al. 2005b; Berntsen et al. 2005; Berntsen et al. 2006a; Berntsen et al. 2006b), and evaluated this new SOM module in the agro-ecosystem model FASSET on a number of independent datasets.

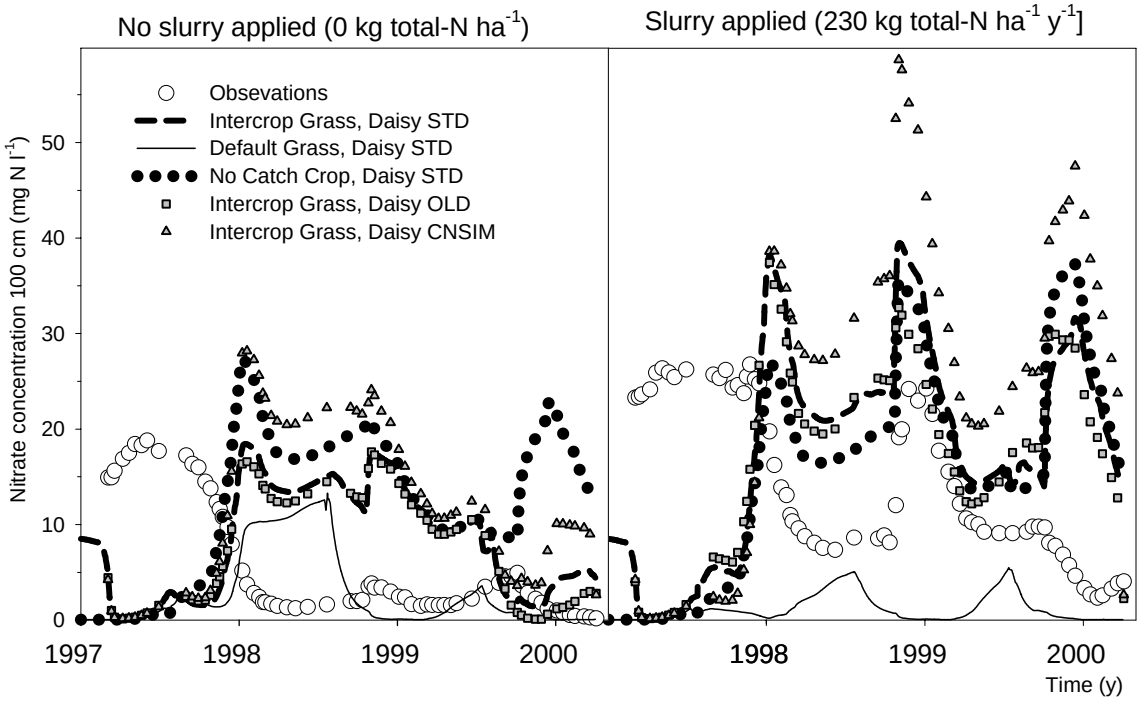

Figure 4.1. Simulation of nitrate concentration at 1 m depth in a 3-year simulation with barley and a ryegrass catch crop. In the 3 previous years (1994-1996), the ryegrass was grazed by dairy cows. The left part of the figure shows the case without fertiliser, while the right shows a fertiliser application of 230 kg total N ha^{-1} y^{-1} as slurry. The scenarios were simulated by three different SOM pool parameterisations in the *Daisy* model, with default spring barley module without ryegrass, a default ryegrass module and a grass module designed for use in intercropping (modified from Paper I).

The simulated temporal pattern and magnitude of cereal and catch crop dry matter production (Figure 2 in Paper I) and nitrogen uptake (Figure 3 in Paper I) after ploughing the ryegrass and grass-clover swards respectively were in reasonable agreement with the

observed values. With the *Daisy* OLD SOM module, biomass production and in particular N uptake were underestimated in all three years for the treatment without slurry application. For the treatments with slurry application, all three SOM modules produced a reasonable fit to observed data. Figure 4.1 shows the nitrate concentration at 1 m depth for the different model simulation aspects. Different SOM setups were tested and the original SOM module parameterisation for *Daisy* (*Daisy* OLD) showed the lowest nitrate concentration. Use of *Daisy* STD parameterisation gave a concentration near the measured, while use of *Daisy* CNSIM parameterisation gave a higher mineralisation and therefore a higher nitrate concentration at 1 m depth. Figure 4.1 also shows nitrate concentration for SOM module *Daisy* STD and use of two different crop parameterisations of a catch crop module (grass) and no use of catch crop. Paper I showed that the dynamics of SOM modules have an effect on the mineralisation and release of mineral N and thus an effect on simulated crop production. However, parameterisations of catch crop modules had a higher effect in calculating nitrate concentration in 1 m depth. This shows that it is important to take all modules into consideration when improving soil plant models.

4.3 Simulated root growth, crop rotation and soil nitrogen dynamics under typical Danish soil conditions

Annual precipitation in Denmark differs greatly over short distances. Figure 4.2 (left), shows a range from 500-550 mm in the eastern part of the country to 800-950 mm in the west. The amount of precipitation varies between years, as well as within years, combining to create significant differences. Aarslev, which is located in the centre of the island Funen, has an annual average of 767 mm (minimum 504 and maximum 1054 mm). Winter precipitation (1 Oct to 31 March) is on average 379 mm (minimum 76 and maximum 651 mm) (31-year mean, 1972-2003). This great variation in precipitation provides a different water amount for plant production in summer, and a surplus of precipitation during winter time. High winter rainfall results in leaching of nitrate from upper to deeper soil layers or even out in drainage water, so it is lost for the next season. In order to avoid N losses to the environment, it is important to select crops with deep rooting growth in the year following a crop where high residual N is expected.

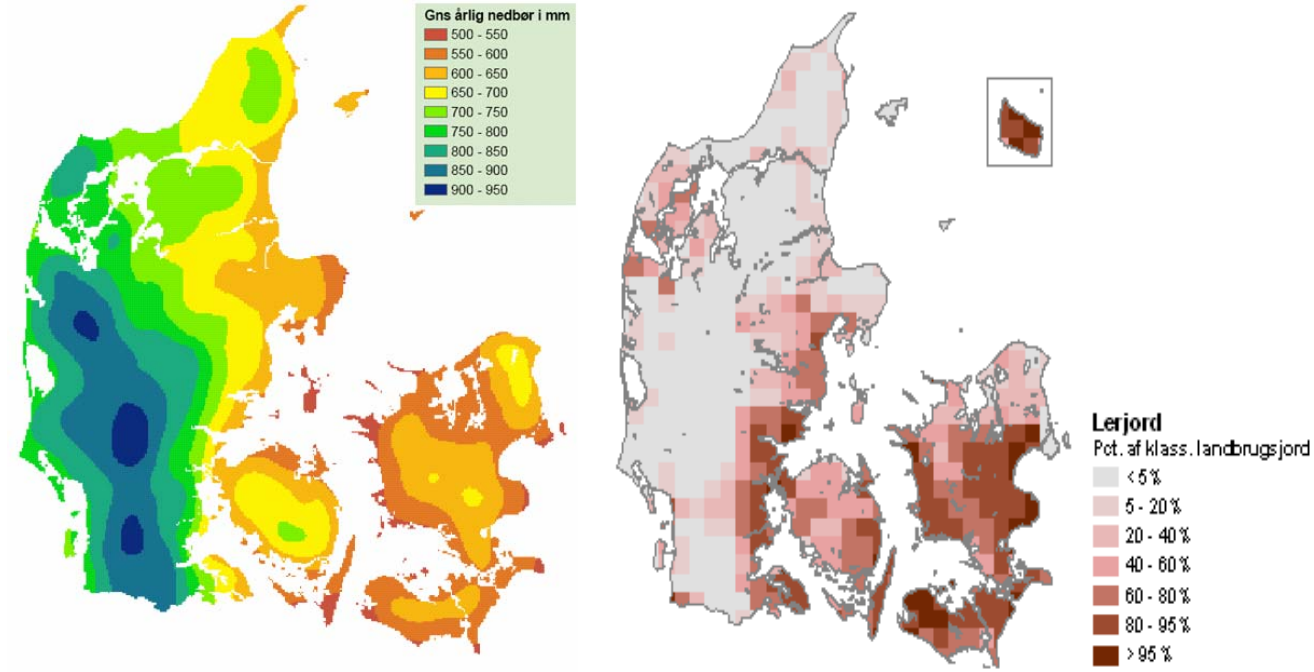

Figure 4.2. Left: Average annual precipitation in Denmark (1960-1989), ranging from 500 mm (red) to 950 mm (dark blue). For precipitation classes see key in figure. Right: Location of clayey soils in Denmark. Dark red indicates a high ratio (>95%) of clayey soils in the grid (20x20 km^2), light gray a low ratio (<5%). Source: www.DJFgeodata.dk.

The clay content of Danish arable soils generally ranges from 3 to 25% (some individual sites above 25%). In Denmark, 34% of soils are coarse or fine sand, 28% clayey sands and 31% sandy clays (Table 4.1). This range in soil texture gives different physical and hydraulic conditions for root development. Water retention curves provide information on the plant-available water content in the range pF 2 to 4.2, which ranges from 10% (v/v) for sandy soils to 24% (v/v) for clays (Borgesen & Schaap 2005).

Danish sandy soils are located in the western part of the country (Figure 4.2, right) as a result of the maximum extent of the ice sheet during the last ice age. Sandy soils have faster drainage and low soil water field capacity, so spring crops can be established earlier in spring. However due to the lower content of micropores, poor aggregate structure in the plough layer and higher soil strength, there is often a shallower rooting depth of 40 to 80 cm for barley and grass on sandy soils. As a consequence, if irrigation is not possible crop yields can be low in years with low precipitation.

Clayey soils have better conditions for root growth, but due to low hydraulic conductivity, the soil is trafficable later in spring. Deep rooting depth and high amounts of plant-available water provide good conditions for high crop production. Root depth in

sandy loams for monocots such as ryegrass, rye and spring barley ranges from 80 to 100 cm, and for dicots such as oilseed rape, oil radish and white cabbage from 200 to 250 cm (Kristensen & Thorup-Kristensen, 2004). However, problems for root development can arise in clayey soil due to compaction by heavy machinery.

Table 4.1. Definition of soil types in the Danish Soil Classification, and distribution of soil types in Denmark

Soil type	Clay <2µm	Silt 2-20 µm	Fine sand 20-200 µm	Total sand 20-2000 µm	Proportion of Danish arable land (%)
Coarse sand	0 – 5	0 – 20	0 – 50	75 – 100	24
Fine sand	0 – 5	0 – 20	50 – 100	75 – 100	10
Clayey sand	5 – 10	0 – 20	0 – 95	65 – 95	28
Sandy clay	10 – 15	0 – 20	0 – 90	55 – 90	24
Clay	15 – 25	0 – 20		40 – 85	7
Organic soil					7

Annual precipitation and precipitation in the winter season show a large variation between years in the different regions of Denmark. Therefore a risk for high leaching losses of nitrate can appear in regions with high clay content in years with high precipitation, while low leaching losses occur in dry years on sandy soils. This is discussed in more detail in section 4.4.

4.4 Nitrate movement and uptake by catch crops

Paper II analysed the effects of catch crop use and rooting depth on nitrate retention as affected by precipitation and soil texture under Danish conditions using simulations covering different soil types, precipitation regimes and catch crops. The simulations were made using the soil-plant-atmosphere model *Daisy* (Abrahamsen & Hansen 2000). The results are used here to answer the following questions:

- How great is nitrate retention in soils with different textural properties in relation to different precipitation regimes when no catch crops are grown?
- What effects do catch crops with different root growth patterns have on nitrate availability and depth distribution in the following spring?
- How does nitrate retention without catch crops compare with catch crop effects on soil N in the following spring?
- Does root depth of the following main crop influence the outcome?

Figure 4.3 shows differences in mineral N content for different soil types, precipitation regimes and use of catch crops. The mineral N content in Figure 4.3 is calculated for 1 May, where the catch crop had been growing from 15 August to 1 December of the previous year. With information on choice of crop in the coming season and knowledge about soil types and precipitation regimes in a particular area, Figure 4.3 can be used to determine whether a catch crop should be grown or not. Sandy loam has a higher soil water-holding capacity and section A2 of Figure 4.3 shows that a deep-rooted crop will have the ability to reach nitrate percolated below 1.0 m in low precipitation conditions and in sandy loam. However if the soil type is a sandy soil (Figure 4.3, section A1) or under a high precipitation regime (Figure 4.3, section B2), the nitrate percolates further down and even a deep-rooted crop will not be able to reach nitrate left in the autumn. In situations with high residual nitrogen in autumn and where the following crop has shallow to medium rooting depth, a catch crop is recommended to empty deeper soil layers of nutrients. Two different catch crop strategies can be used, non-winter hardy

crops such as some *Brassica* species or winter-hardy crops such as grasses. *Brassica* species have a fast root penetration rate and high root density in the whole root zone and have a high potential N uptake, but often the crop dies off early in winter. Under some conditions, high mineralisation takes place and high precipitation can leach nitrate below the root zone. In such cases winter-hardy crops can be used, so mineralisation of crop litter will take place later in spring to avoid this leaching. A negative effect of using catch crops can be observed in dry winters where nitrate only percolates a short distance and catch crop litter can bind nitrogen in organic matter, rendering it unavailable in the first part of the growing season. This interaction is called the *pre-emptive effect*.

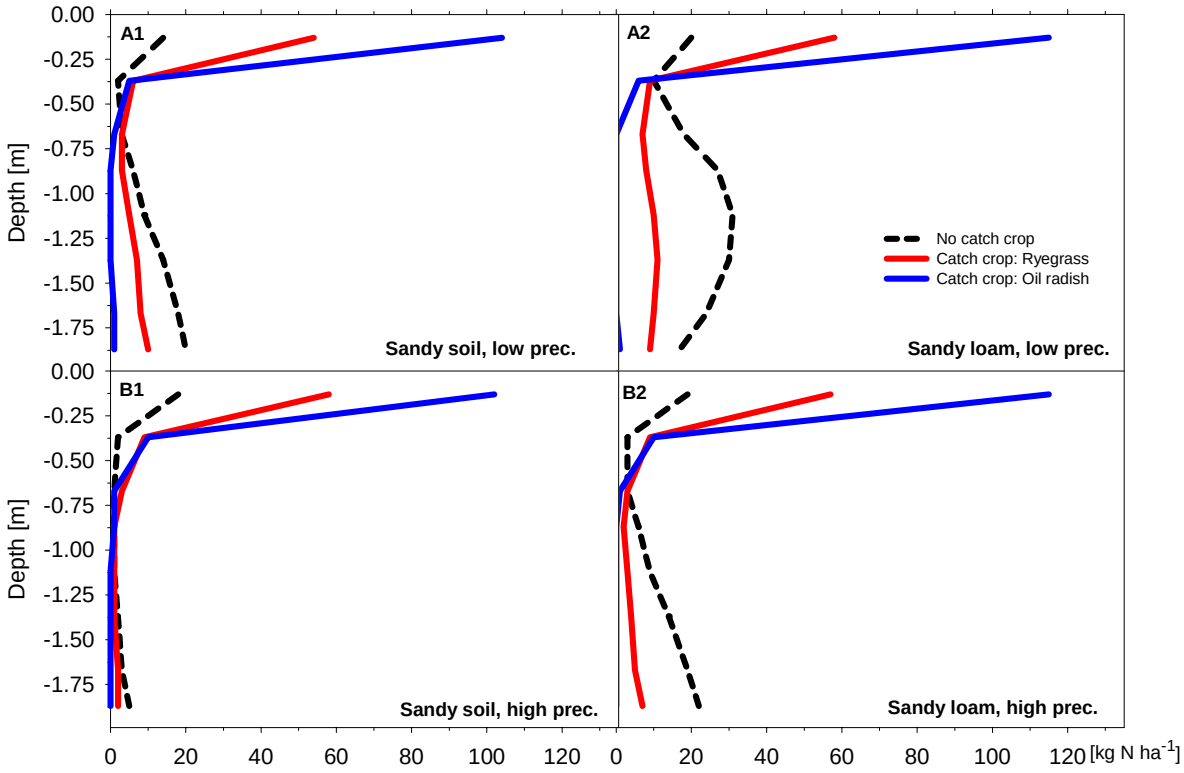

Figure 4.3. Mineral N content on 1 May for two soil types, two precipitation regimes and a grass or oil radish catch crop or no catch crop. Mineralisation from catch crop residues increased mineral N in the topsoil layer in spring. Oil radish was best at taking up N in the whole soil profile. In the sand and sandy loam soils, part of the nitrate was leached further down before roots had developed into those soil layers. For the low precipitation regime and the sandy soil, the N front reached 1.25 m depth. A deep-rooted main crop in the following year would be able to take up this N, and a catch crop would not be necessary. Source: Pedersen et al. (2005).

Paper II showed that winter nitrate retention in the 0-0.25 m and 0.25-0.75 m layers was low in all textural classes and precipitation regimes studied. In the 0.75-2.0 m layer, the loamy sand and sandy loam had a higher degree of retention, especially in the medium and low precipitation regimes. Catch crops with shallow root systems extracted less

nitrogen from deeper soil layers than deep-rooted catch crops and this nitrogen was leached to below 2.0 m during winter and spring on the sandy soil and in high precipitation regimes. The mineral N content in spring (1 May) was higher in the upper part of the soil profile after growing either of the catch crops in autumn compared with no catch crop for the three soil types. On the loamy sand and sandy loam soils in the medium and low precipitation regimes, the mineral N content in the 0-2.0 m soil layer was generally high with no catch crop. In such cases, a deep-rooted main crop in spring could have the ability to reach nitrate in the soil profile, and thus a catch crop in the previous autumn could result in less nitrogen being available for the following crop. When growing crops with shallow root systems, catch crops always provide an advantage as regards nutrient management.

5 Modelling plant root development and N uptake

For prediction of plant growth, water movement and N pools, dynamic models can be a useful tool in understanding the effects of interaction between different factors on the different crop and soil functions. However, a plant soil model is only a simplification and can only explain a small part of what really happens, and it is necessary to introduce further simplifications into the system to make it amenable to mathematical solution (Van Wijk 1963). The single components in the model have to be calibrated and validated with the behaviour of the real system for which the model is intended to make predictions. Such evaluation is very important for each component of the model in order to achieve the best prediction (Rykiel 1996). Soil plant models often contain a soil module that includes information for physical conditions such as bulk density, texture, pore space and hydraulic conditions. Furthermore, a simulation of plant growth in a dynamic model needs a driving variable such as days, temperature, precipitation, or solar radiation (Faivre et al. 2004). Modules are often spilt up into sub-modules so that users are able to specify simulation after scale and available field data, for instance the *Daisy* model with various water models for calculation of water percolation (Hansen et al. 1991).

5.1 Simulations of root growth and development

Prediction of root growth and root function is essential in modelling plant growth and performance, and for detailed modelling calculations are spilt into different steps. Each step can be modelled in a more or less sophisticated way and can be validated with field trials provided that the state variables correspond to measurable entries. When calculating root growth and root density in soil profiles, it is important to have information about the root/shoot ratio in order to estimate root biomass and root length.

A range of models for root simulations are presented in the literature. The models are often tailored for a specific issue, which may be architectural root simulation of a single crop species, uptake of water or a single nutrient, e.g. N, P, K, or micronutrient. Some models are used for a single crop species. Other models are plant-soil-atmosphere models that include a root sub-module for simulation of many different crop species on a large scale.

Architectural root models are 3-D models, which are created for a better understanding of the architectural importance of roots and special for nutrient acquisition. SimRoot is an architectural root model that has been developed for simulation of different root systems and quantification of root-related parameters such as phosphorus uptake by bean and corn roots in non-homogeneous soils (Ho et al. 2004; Lynch 1995; Lynch et al. 2007). Another model is the 3-D model ROOTMAP, which is used to investigate the water and nutrient uptake by cereal crops on a small scale in soil by modelling root branching (Diggle 1988). The model has sub-modules for soil, soil water and nutrient dynamics, and root development can be affected by conditions in those sub-modules. The ROOTMAP model has been evaluated with field data and used to investigate root density in the root profile against nitrate leaching (Dunbabin et al. 2003; Dunbabin et al. 2002).

A soil-atmosphere model could be the SPACSYS model (Wu et al. 2007). This is a multi-dimensional, field scale, weather-driven dynamic simulation model of C and N cycling between plant, soil and microbiology and the model operates with a daily time-step. The root modelling is spilt in two parts, one for branching position and one for branching orientation. The model uses parameters for determining branch orientation vertically and horizontally that have been built in from SIMROOT and a 3-D root model developed by Pages for simulating the maize root system (Lynch et al. 2007; Pages & Pellerin 1996; Pages et al. 2004).

In the plant-soil-atmosphere model *Daisy*, which is a 1-D model, root depth is calculated by using day-degrees and root density profile is calculated on a daily basis using the Gerwitz & Page equation (Gerwitz & Page 1974; Abrahamsen & Hansen 2000). The crop model calculates daily N demand and the soil model available N using information on root depth and root density. N uptake is assumed to be the N flux towards the cylinder formed around the root surface. The model calculates both ammonium and nitrate, and ammonium is assumed to be preferred before nitrate. *Daisy* has now been updated for a new 2-D implementation and is available at the model homepage (http://www.dina.kvl.dk/~*daisy*/).

Prediction of root growth and root function is essential in modelling plant growth and performance, and for detailed modelling calculations are split into different steps. Each step can be modelled in a more or less sophisticated way and can be validated with field trials provided that the state variables correspond to measurable entries. When calculating root growth and root density in soil profiles, it is important to have information about the root/shoot ratio in order to estimate root biomass and root length.

Root penetration rate and rooting depth of plants are important issues for root modelling. The penetration rate determines when roots extend into new soil layers and increase the potential soil volume for nutrient and water uptake. When a root depth is calculated, calculated root biomass can be distributed in the soil profile. Section 5.2 illustrates the considerations behind the development of a root sub-module for a plant soil model and briefly covers aboveground growth, root/shoot distribution, root penetration calculation, root density calculation and N uptake in models.

5.2 Root growth vs. shoot growth

In the soil-plant-atmosphere continuum, plant growth may be considered the result of interactions between biological, chemical and physical processes. The canopy intercepts incident solar radiation and CO_2 is assimilated from the atmosphere and transformed into carbohydrates. During biochemical conversion of assimilates into new proteins, structural tissue materials and maintenance carbohydrates, CO_2 is released by growth and maintenance respiration. In addition, and particularly in C3 plants, up to 50% of photosynthetically assimilated carbon may be released by photorespiration.

The *Daisy* model (Hansen et al. 1990; Hansen et al. 1991) simulates canopy gross photosynthesis from the intensity of photosynthetically active radiation intercepted by the crop and the efficiency by which the absorbed radiation is converted to carbohydrates at actual temperature. The growth rate can be simulated as shown in Equation 3:

$$\partial Y / \partial t = \gamma \left(F_{g,f} - r_m W \right) \qquad \text{Equation 3}$$

where Y=growth rate, $F_{g,d}$ = Canopy gross photosynthesis, r_m = root biomass, W = Total dry matter. The assimilate partitioning between shoot and root in annual crops such as cereals and rape follows a pattern determined by plant species and physiological age. For example the *Daisy* model expresses the latter in terms of temperature sum initiated at crop emergence.

The carbohydrate translocated to roots is used to increase the quantity of root biomass, nutrient uptake, symbioses with e.g. mycorrhizae, maintenance and growth respiration, and release of organic compounds to the rhizosphere. The relationship between root length and shoot can be expressed thus:

$$L_r = \alpha \left(W_s\right)^{\beta} \qquad \text{Equation 4}$$

$$\ln L_r = \beta \ln W_s + \ln \alpha \qquad \text{Equation 5}$$

where L_r = total root length, $.\alpha$ = distribution ratio, W_s = shoot dry matter, β = algometric growth ratio. This implies that relative growth rate of the shoot biomass (RGR_S) and root length can be expressed thus:

$$RL_rW_r = \beta * RGW_r \qquad \text{Equation 6}$$

$$RL_rW_r = \frac{1}{L_r}\partial L_t \Big/ \partial t; \quad RGW_s = \frac{1}{Y_S}\partial W_S \Big/ \partial t \qquad \text{Equation 7}$$

where RL_rW_r = Relative growth rate for root length , β = algometric growth ratio, RGW_s = Relative growth rate for shoot, L_r = total root length, W_s = shoot dry matter, t = time. Root length is thus calculated in the model and then the model has to calculate the rate of root elongation and the extension of the root system for root density calculations.

5.3 Root depth, density and nitrogen uptake

The aims of Paper III were to model root development, root density and N uptake in the soil profile and especially to make it possible to model uptake in deeper soil layers. The specific objective was to determine whether a simple and manageable equation could be used to reflect root density observations in the field and the associated N uptake in a large range of different crop species.

The model was tested with different parameter settings and constructions to analyse the sensitivity. From a user-friendly point of view, the aim for the root sub-module was to only adjust a few parameters when using the model for simulation of a range of different crop species.

The crop model for calculating growth, biomass and N demand was developed by Greenwood and co-workers (Greenwood et al. 1996; Greenwood et al. 2001). Here we input the required dry matter and N content on the day of harvest, and equations managing biomass increase and N content by daily calculation of N and water uptake. When N and water demands are not fulfilled a biomass reduction takes place.

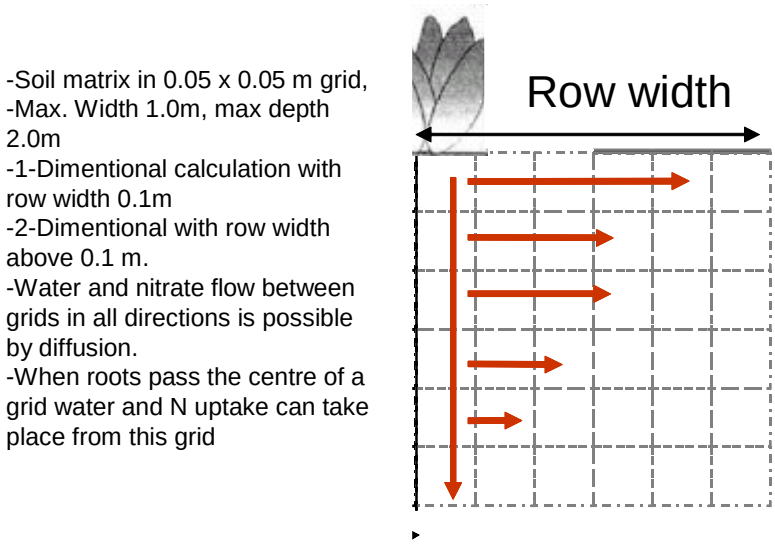

Figure 5.1. Schematic illustration of root density calculation and information on the soil model and how the division into grids influences calculation of root development.

Figure 5.1 shows how the soil matrix is spilt up into grids and provides a short introduction to calculations outside the root module. The root model requires daily information on aboveground biomass and N demand and potential N accumulation.

Rate of root penetration rate can be affected by root age, plant type and phenological stage (Rose 1983). However, other field data indicate that root penetration rate can be described more simply by a factor and day-degrees (Kage et al. 2000; Kristensen & Thorup-Kristensen 2004). A lag phase for sowing or planting seedlings is calculated in day-degrees between minimum and maximum temperature as shown in Equation 8:

$$DD = \sum T = \begin{cases} 0 & ;T_{air} \le T_{\min} \\ T_{air} & ;T_{\max} \le T_{air} > T_{\min} \\ T_{\max} & ;T_{\max} < T_{air} \end{cases} \qquad \text{Equation 8}$$

where DD = Degree days, T_{air} = air temperature, T_{min} = minimum temperature, T_{max} = maximum temperature. Equation 9 calculates root penetration depth (R_z) and, similarly to horizontal growth, R_z has to pass beyond half the vertical depth of a grid before roots start to grow into horizontal grids.

$$R_z = \begin{cases} R_{\text{z-min}} & ; \sum DD \le DD_{lag} \\ \sum ((DD - DD_{lag})k_{rz}) + R_{\text{z-min}} & ; \sum DD > DD_{lag} \\ R_{\text{z}-\max} & ; \sum D - DD_{lag} k_{rz} + R_{\text{z-min}} > R_{\text{z}-\max} \end{cases} \qquad \text{Equation 9}$$

Where R_z = root depth, DD_{lag} = lagphase in degree days, k_{rz} root penetration rate into depth, $R_{z\text{-}min}$ = Starting depth, $R_{z\text{-}min}$= maximum rooting depth.

Root density

The total root length is calculated by assuming a specific root length density S_r. In Equation 8, total root length is calculated. Root density is calculated according to Gerwitz and Page (Gerwitz & Page 1974) and modification of the Hansen al. (1990) model as shown in Equation 11. The root density calculation is modified by adding an effective root depth q, which is $1.3R_z$. Here root density decreases from the root density value at the calculated root depth to zero at the end of the q part. Root density distribution in one dimension within the same root biomass but calculated with four different values of form parameter a_z is shown in Figure 5.2.

$$L_r = W_r S_r \qquad \text{Equation 10}$$

$$L_z = \begin{cases} L_0 e^{(a_z z)} & \text{z} < \text{R}_z \quad ; z < R_z \\ L_0 e^{(a_z R_z)} \left(1 - \dfrac{z - R_z}{qR_z - R_z}\right) & ; q\text{R}_z > z > R_z \\ 0 & ; \text{z} > q\text{R}_z \end{cases} \qquad \text{Equation 11}$$

Where S_r = Specific root density, q = linearly declining part in root density below calculated root depth.

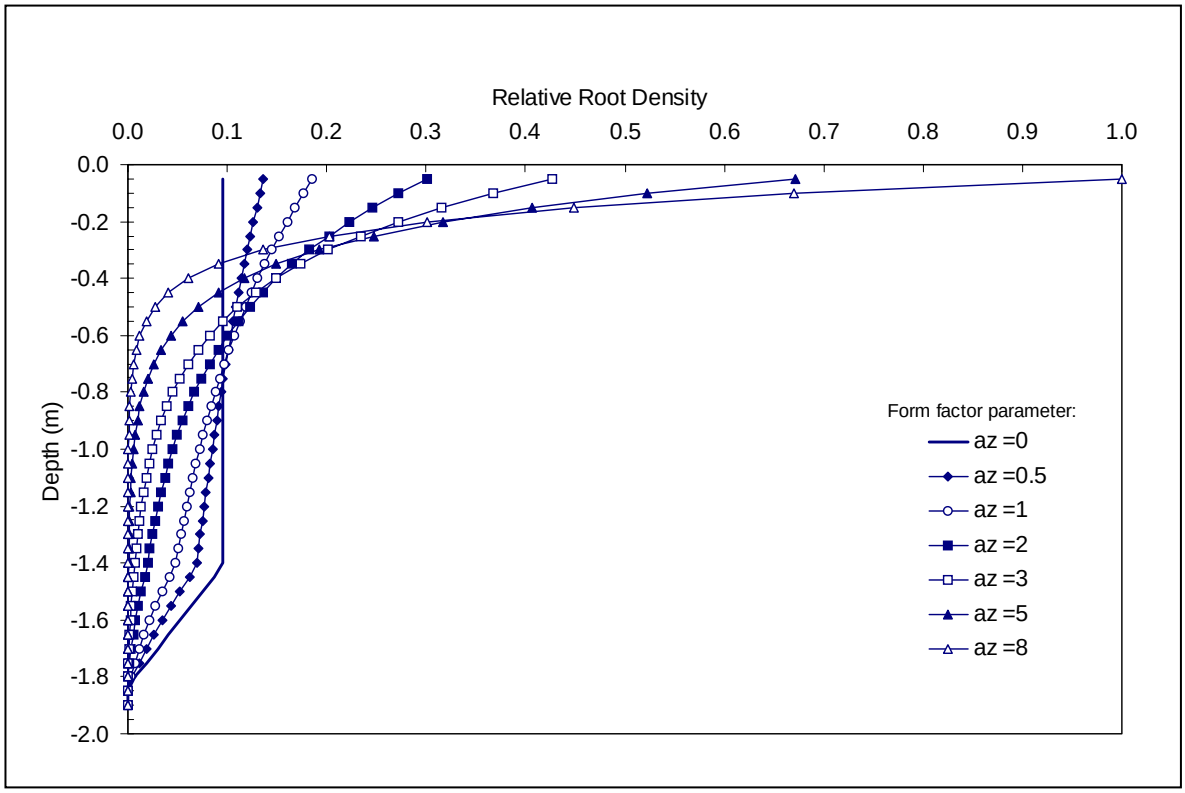

Figure 5.2. Relative root density distribution in the soil profile for a root model simulation after 110 days with different form factors. The total root length is identical for different simulations. Default setting of root parameters includes q =1.3.

Figure 5.2 shows how a_z controls root density in the soil profile from very high near the surface (a_z =8) to a even distribution of roots from the top layer to calculated rooting depth (a_z =0). Root depth (R_z) was calculated to 1.4 m in Figure 5.2, while below this depth we tested a modification of the default module whereby the root density increased linearly from root depth to a new soil depth, which was controlled by q and here was q=1.3 times. By using values for a_z from 0 to 8, root density distribution can be equally distributed or all roots can be placed in the surface soil layer. Comparing modelled root density with measured root intensity, root frequency or root density in Figures 3.5 and 3.6 shows an agreement with monocot species such as leek (*Allium porrum*), rye, oats and ryegrass for form parameters 3 and 8. Comparing measured values for dicot species such as rape, cabbage and radish and winter rape showed an agreement with form parameters 0 and 1. However measured data sometimes show increasing root frequency from 0.5 to 1.5 m depth, which the root model is not able to manage (cabbage Figure 3.6b). Figure 5.3 shows root density distribution for use of the equation in two dimensions. First, root length is distributed into depth and then into width. By the form parameter a_z it is possible to simulate different root density patterns observed in field studies.

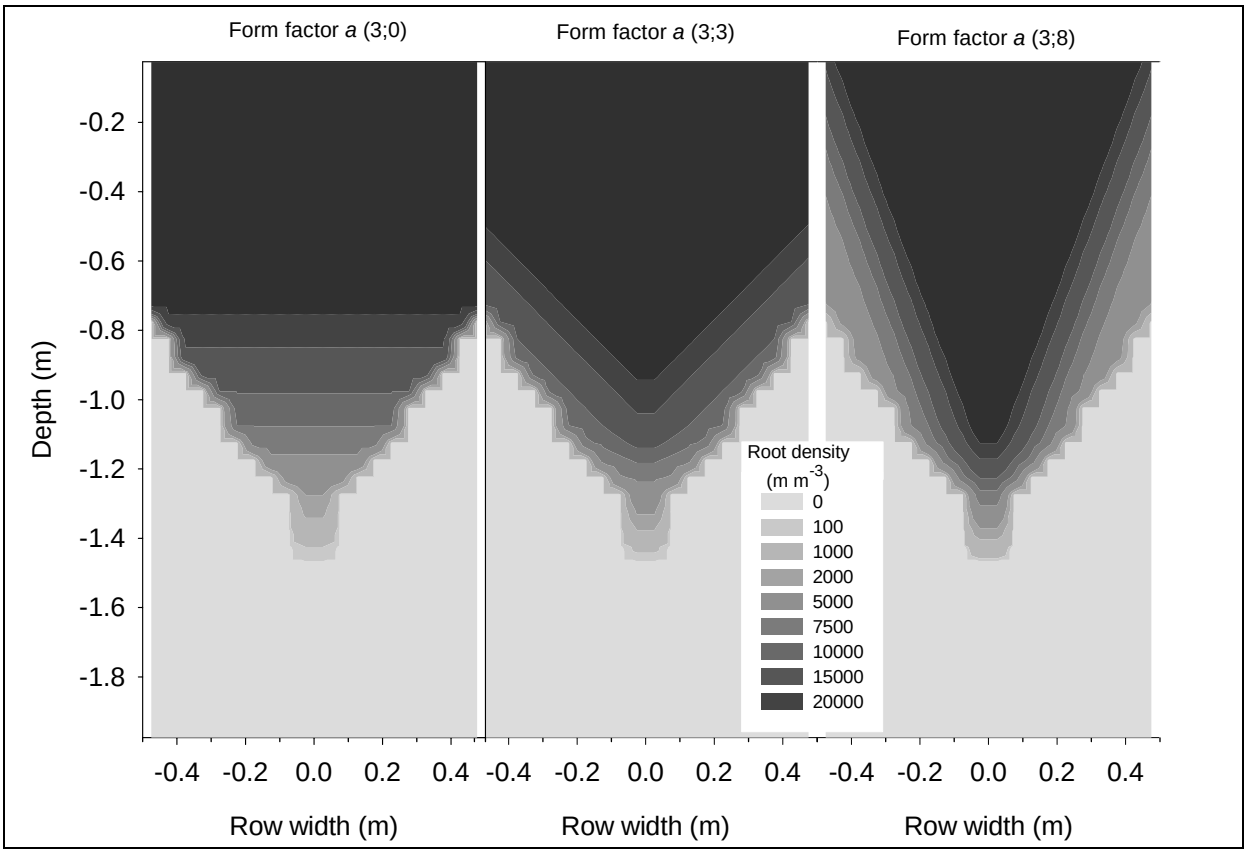

Figure 5.3. Root density in the soil profile in a two-dimensional system. Three different form parameter settings were used in two dimensions: (a_z;a_x), (3;0), (3;3), (3;8). Decreasing root density is indicated by decreasing intensity of shading.

Nitrogen uptake in the model

Some of the models assume a uniform distribution of roots in soil and this is used to calculate a mean radius for single roots. A high root density gives a shorter distance between roots and a smaller radius of the soil cylinder, which gives a faster uptake of water and nutrients. In the upper soil layer, roots are present at such high density that this extra calculation only has a minor effect because roots are so close to each other. In deeper soil layers roots are not uniformly distributed, especially in poorly structured soils.

Potential N uptake is calculated for ammonia and nitrate in each soil unit using root length as shown for nitrate in Equation 12, modified from Nielsen & Barber (1978).

$$N_{pot}(NO_3^-) = \frac{L_r kN (c_{NO_3^-} - c_{\min\_NO_3^-})}{kf + c_{NO_3^-}} \qquad \text{Equation 12}$$

Where $N_{pot}(NO_3^-)$ = potential nitrate uptake, kN and kf = N uptake factor, $c_{min\ NO3-}$ = Nitrate unavailable for plant uptake, c_{NO3-} = concentration of nitrate. Actual daily N uptake is

calculated from the potential N uptake and the N demand using Equation 13. This equation manages the N uptake and avoids extremely high N uptake the day after a fertilisation event where the potential N uptake has been low and N demand high for a period:

$$N_{up} = N_{demand}\left(1 - e^{\left(-m_N\left(\frac{N_{pot}(NO_3^-) + N_{pot}(NH_4^+)}{N_{demand}}\right)\right)}\right) \quad \text{Equation 13}$$

Where N_{up} = actual nitrate uptake, N_{demand} = Nitrogen demand, m_N Parameter to adjust daily N uptake (default parameter value for m_N = 1), $N_{pot}(NO_3^-)$ = potential nitrate uptake. In Figure 5.4 the N uptake ratio is shown, the figure illustrate Equation 13 and that the m_N determine had large fraction of the potential available N the roots was able to take up. When m_N was above 1 the model will make fast respond on the N demand, whereas a value below 1 will result in a slower uptake and it will take a longer period to fulfil the N demand.

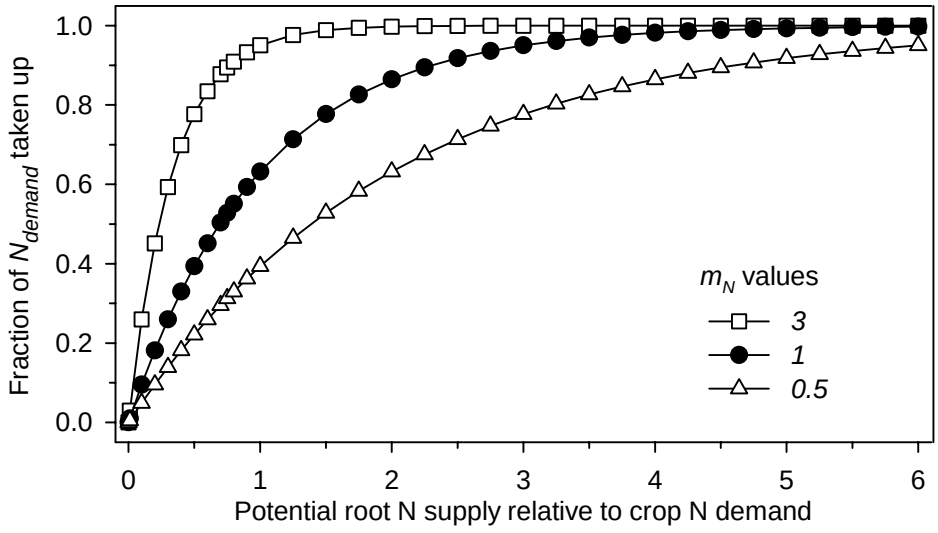

Figure 5.4. Regulation of root N uptake in the root model. Illustration of a slow (m_N =0.5), fast (m_N = 3) and the default parameter value (m_N = 1) for m_N parameter in Equation 13. The equation is used to calculate the actual daily N uptake.

The availability of mineral N to plants depends not only on soil N concentration, but also on the root density. Under field conditions, N uptake by arable crops can be fast in the first few days after fertiliser application, mainly by the roots near the soil surface (Breland 1996). The model

simulation of N depletion after fertiliser N application was somewhat slower or similar to field data depending on the form parameter where a_z =8 shows the fastest response and a_z = 0 slowest (Figure 5.5). This may affect the N balance in a situation with shallow-rooted crops, especially in a sandy soil and under high precipitation events. The plant model also predicted a lower mineral N content in the surface layer in autumn after harvest. This difference can be the result of decomposition of dead leaves during the last part of the season, which the model in the current version does not take appropriately into account.

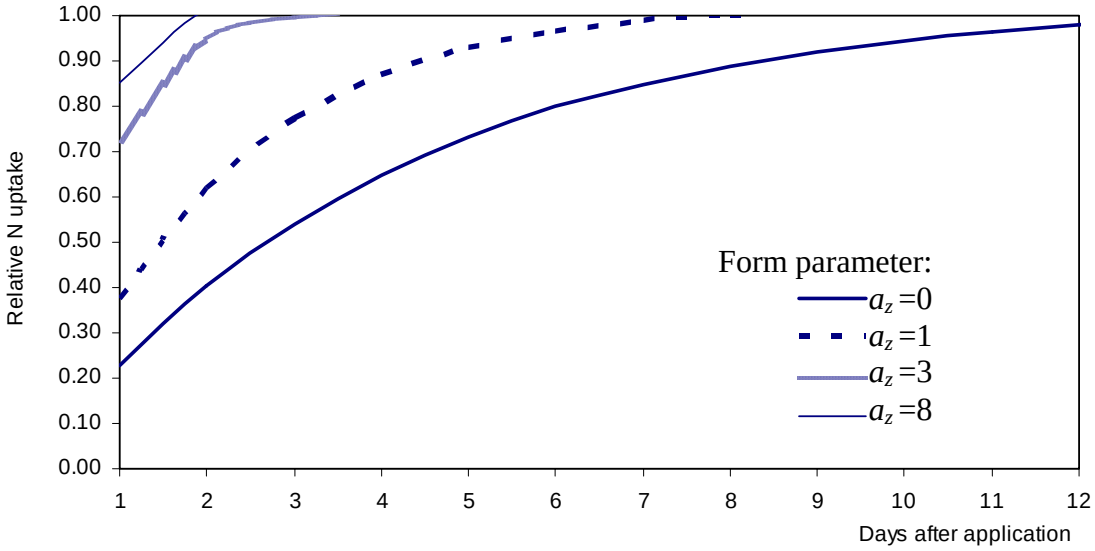

Figure 5.5. Relative N uptake after surface application. Simulation where soil N level was below optimal N uptake for the crop. Nitrogen was added as nitrate on day 90 in a simulation with four different values of a_z and m_N = 1. Key to symbols see figure.

Figure 5.6 shows relative N content at four soil depths in a simulation with three different form parameters and root penetration rates. Figure 5.6 shows how the model is able to deplete the soil layer of mineral N differently with different values of the form parameter, especially in the 1.0-1.5 m soil layer, where use of form parameter 0 depleted the layer and the simulation with form parameter 8 had no practical importance at the end of the simulation. In the simulation with three different root penetration rates, relative N depletion was affected in all soil layers. In the 0.5 to 1.0 m soil layer the simulation for the slowest (66%) rate showed a later depletion in the 1.0 to 1.5 m layer and only a low depletion late in the simulation in the 1.5 to 2.0 m layer.

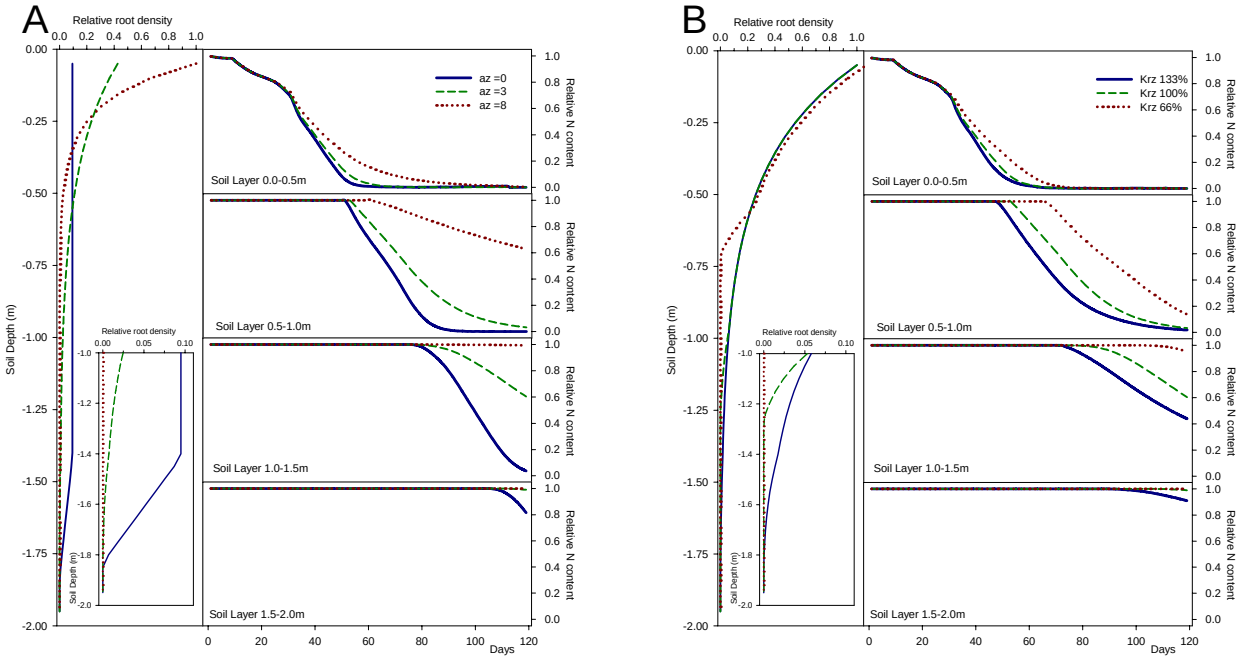

Figure 5.6. Simulation of relative soil N content in four soil layers in a 120-day period for three different a_z values (A) and three different root penetration rates for a_z =3 (B). Root density profile (left part in each figure) is relative root density distribution at day 120. Mineral N content in soil was below potential N demand for the crop. Key to symbols within figure.

During the early growing season, root density often had high root density in soil layer near surface, but the root density distribution can be changed to a higher root density in deeper soil layers towards maturity, shown here for white cabbage in Figure 5.7A,B and C where root density was high day 46 and 64 and fit a high a_z parameter but after 153 days the with cabbage had a more equal root distribution into depth and fit a low a_z parameter. This trend has been observed in groundnut, cauliflower, parsnip, turnip but not in cowpea, lettuce and onion by Greenwood et al. (1982) and Adiku et al. (1996). To further test the effect of the form parameter on N uptake, simulations with two staged form parameter values during growth were carried out. In the early growth stages the model simulated the main part of roots near the surface (a_z =8 for 0 to 500 DD), and thereafter the form parameter was linearly reduced to a given value (from 500 DD to 900 DD). The simulations showed that when the form parameter changed from 8 to 0 or 3 after 500 DD (Day 45), the N depletion from soil layers was faster for a period but ended a level below the simulation result obtained with a constant form parameter (Figure 5.7D). For the case of a_z = 8, N uptake does not satisfy N demand in the beginning of the growing season, and the above ground dry matter production is therefore reduced in this period (data not shown). This reduction has a profound effect not only on aboveground

dry matter production later on in the season, but also on the root dry weight, which relates to the total root length, and thus the potential for N uptake is reduced.

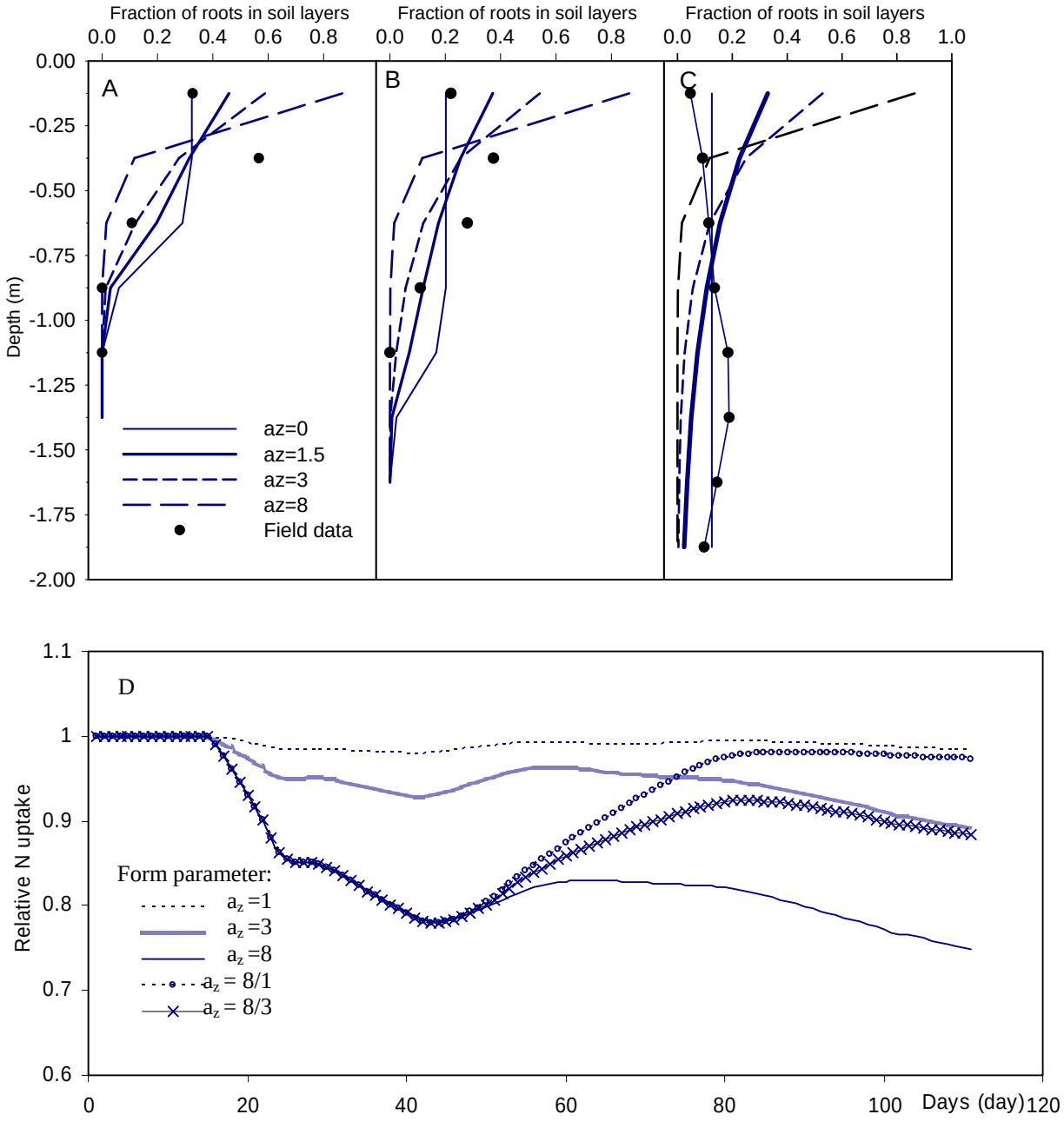

Figure 5.7. Comparison of field root intensity with simulated data of form parameter a_z. Root intensity in the field was measured at harvest as root intersection of grid in minirhizotrons below white cabbage crop and the fraction is calculated in 0.25 m soil layers in A) 46, B) 64 and C) 153 days after planting of white cabbage. Measured data are an average of five fertiliser levels with 3 replications. Simulated data are root density shown as relative root density distribution in soil layers (Source: Paper III). D) Relative N uptake for comparison of a_z =0 default model with a_z =1, a_z =3, a_z =8 and modified root model with a_z =8 going to a_z =1 and a_z =0 going to a_z =3 in the 0-2.0 m soil layer. For more information about modified model see text. For key to symbols see figure.

Such a change in root density in the season could theoretically be important for N uptake and plant production if high precipitation events happen early in the season. The

simulations indicate that this shift in root density below the surface layer has no significant influence on the final yield and N level in the crop at harvest, provided that there is no leaching in the growing season.

In the present model, simulated root depth and development in the soil profile was unaffected by dry conditions and soil bulk density. The error resulting from this simplification is often small in the first part of the season, as the model is designed to be used for horticultural and agricultural crop simulations where soil moisture often remains at field capacity during spring under humid climate conditions or with use of irrigation. Furthermore, even if the soil contains compact layers with high soil bulk density and high soil strength, plants still often have possibilities to penetrate such layers though cracks, worm holes and old root channels, while a range of plant species have been found to have roots capable of penetrating hard layers (Rosolem et al. 2002; Materechera et al. 1991). In addition, Kirkegaard and Lilley (2007) found that 30-40% of the roots of winter wheat occurred in biopores and cracks in the 0.2-1.0 m soil layer.

Modelling N depletion from field data

In a field experiment, white cabbage was transplanted on 18 April and harvested on 21 October 2004. Soil mineral N was measured on 12 May (mineral N in model adjusted to these data), 20 July and 26 October 2004. For this study we selected five fertiliser levels (A to E) from this experiment. These were (where Y_1 is N application to the preceding cauliflower crop in 2003, Y_2 is N application to white cabbage on 18 May 2004, and the numbers are kg mineral N ha^{-1}): A: $Y_1 0 Y_2 0$; B: $Y_1 230 Y_2 0$; C: $Y_1 0 Y_2 120$; D: $Y_1 230 Y_2 120$; and E: $Y_1 390 Y_2 120$. The different fertiliser applications in the preceding year gave different levels of available N in topsoil and subsoil and therefore an opportunity to analyse the ability of cabbage for deep N uptake. The experiment is still unpublished but information about soil and site has been reported elsewhere (Thorup-Kristensen 2006). The simulations showed lower N uptake on 20 July, when simulated mineral N content was higher than measured. At this stage the differences between a_z values or fertiliser levels are small (Figure 5.8A1, B1). After harvest and under low N conditions the simulation for a_z =0, 1 and 1.5 emptied the soil profile as did the measured field data, but higher a_z values did not reproduce the measured depletion in subsoil

(Figure 5.8A2). At high soil N conditions the simulation with a_z=0 and 1 did not empty the surface soil layer (0-1.0m) satisfactorily, whereas the simulations with a_z=5 to 8 had too high N uptake (Figure 5.8B2). In the subsoil, the simulations with a_z=1, 1.5 and 2 fitted the measured data best. The results showed that a_z=0 and 1 gave too few roots in the 0-1.0 m soil layer for satisfactory N uptake, while below 1.0 m, a_z higher than 3 gave too low root density and too weak N uptake. The conclusion was thus that a_z=1.5 was the best value. An analysis for all a_z values tested in the five selected fertiliser levels confirmed this, as a_z=1.5 had the best fit with lowest RMSE value for the subsoil (calculated on measured mineral N vs. predicted mineral N).

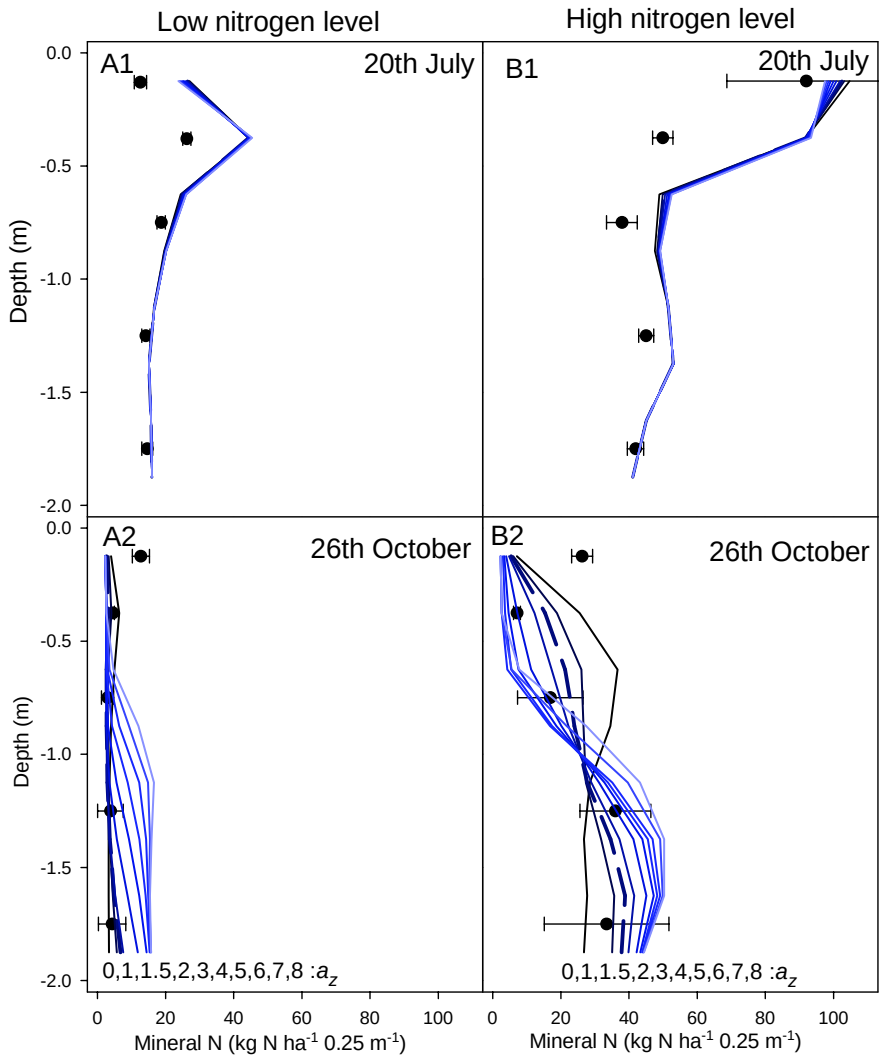

Figure 5.8. Test of a_z parameter for white cabbage on field data with low (A: fertiliser level A) and high (B: fertiliser level E) nitrogen level in spring. White cabbage was planted 18 May and harvested 21 October. Soil mineral N measured 20 May or 26 October (black circles, n=3, bar standard error), curves are simulations with different a_z values (0, 1, 1.5, 2, 3…8) See figure for simulation order. The best fit was a_z =1.5 dashed dark blue line.

The validity of the model with different crops was tested against data from another field experiment. Leek, red beet (*Beta vulgaris var. conditiva*) and white cabbage were grown for two years after a ryegrass catch crop or no catch crop in the preceding autumn. Dry matter and N uptake were measured at harvest and mineral N in the soil was measured on 18 May and 31 October in 2001 and 16 May and 30 October in 2002. A detailed description of the experiment is given in Thorup-Kristensen (2006). The simulations for the three crops were adjusted to reproduce measured N uptake in the field. The field experiment included two catch crop strategies in the year preceding the three crops, which resulted in two different soil mineral N profiles in spring. Field data in spring for no catch crop showed a high mineral N level below 1.0 m depth and a high mineral N level in the surface layer for use of ryegrass as shown with open circles in Figure 5.9. This is common on this soil texture class and precipitation regime, as shown in Figure 4.3A2.

Root frequency measurements for the field experiment are shown in Figure 3.6B. Leek had a high root frequency near the surface and a low rooting depth, which fits well with the root model and $a_z = 8$. Red beet and cabbage had a rooting depth to around 2.5 m and a high root frequency until 2.0 m (Figure 3.6B). A simulation with a low a_z value, e.g. 1.5, placed the majority of the roots in the surface layer, as did an exponential equation, but a high root density was still produced in deeper layers. This meant that field measurements of root frequency and root density calculation by the model did not agree fully, but there was still a considerable root density in deeper soil layers.

The simulated N depletion after leek corresponded fairly well with measured data. Leek takes up N in the surface layer (0-0.6m) and below this depth N content was determined by the actual leaching, which the simulation managed to match to field data. Red beet had a rooting depth of around 2.0 m, with a medium to high root frequency to 1.5 m and decreasing frequency below.

Measured data for mineral N after harvest confirmed that N depletion follows root frequency. The simulations of red beet showed the same pattern, with a higher mineral N in subsoil below 1.5 m, but the simulation depleted the soil more than field data, except

after ryegrass 2001, which fitted well. Simulation of mineral N after cabbage fitted well with field observations, which meant a high N uptake in the whole soil profile.

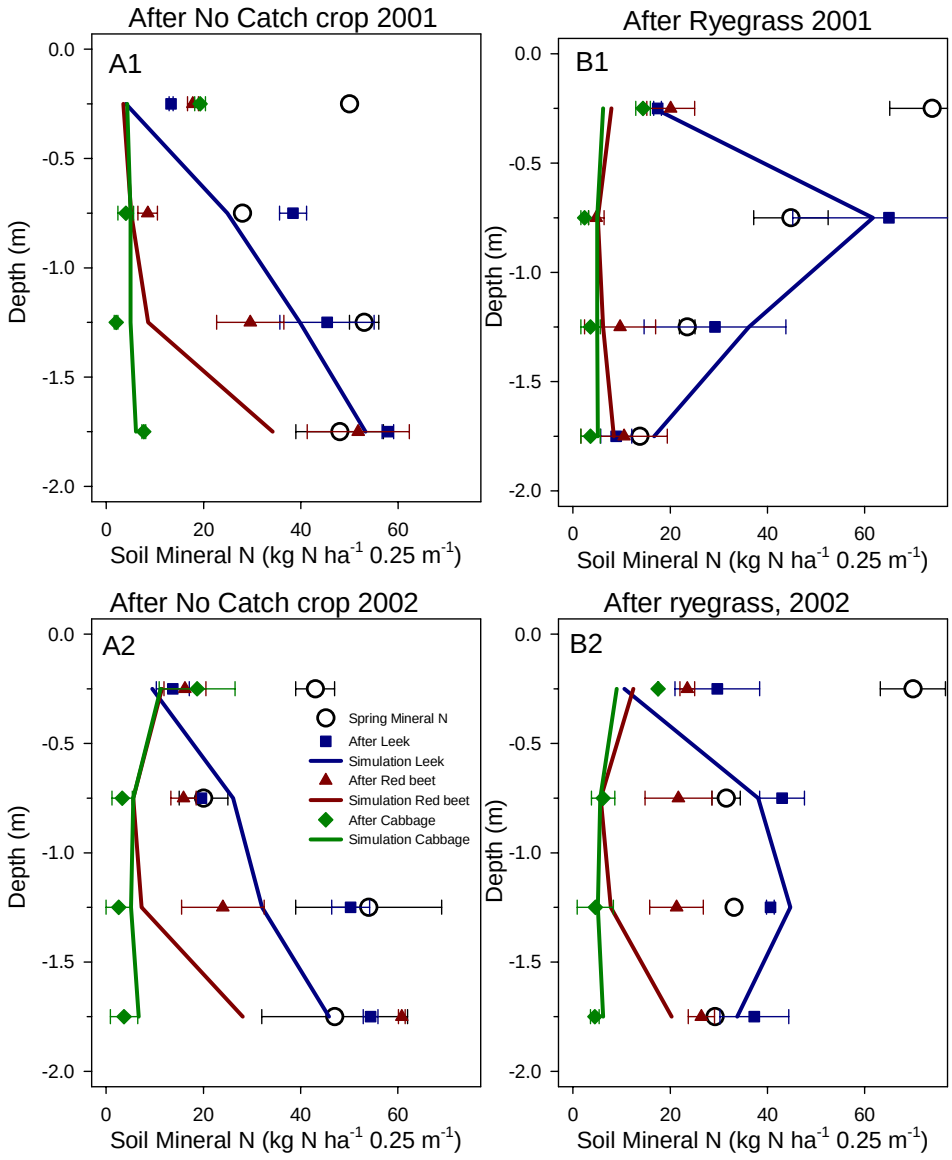

Figure 5.9. Comparison of field mineral N data with model simulations of leek, red beet and cabbage in two years after no catch crop or after a ryegrass catch crop. For key to symbols see A2.

Paper III and the above describe the root module with a simple setup of a well-known root distribution model. When the main factor in the distribution calculations is the form parameter, it is possible to change the distribution of root density in the different soil layers. The simulated root density was adapted to match some monocot species but not all dicot species. The crop simulations were able to reproduce mineral N depletion in the whole soil profile.

6 Conclusions

In intensive crop production systems there is always a risk of nitrate losses to groundwater or the aquatic environment. This thesis describes model parameterisation and module construction and provides the following suggestions for improving modelling of root development and N uptake in the soil profile:

- Comparison of the influence of SOM modules versus crop modules demonstrated that the simulation of nitrate concentration was more affected by the choice of crop module (different parameterisation) for simulating catch crop than by different SOM modules (differing in both structure and parameterisation).

- The simulations showed low nitrate retention in topsoil layers in all three climatic regimes and soil texture classes examined. Nitrate retention increased greatly with depth in all soil types under low precipitation, while with higher precipitation this increase was mainly seen on soils with higher clay content. The patterns corresponded well with those reported in field trials. Variation in nitrate retention was greatly affected by the variation in precipitation between years

- Use of catch crop, regardless of the rooting depth, gave the same nitrate distribution in spring, with high N content in the surface layer. Deep-rooted catch crops had a potentially higher N uptake in autumn and therefore higher N mineralisation over the next growing season.

- In soils with high water retention combined with years of low precipitation, nitrate was retained in soil layers above 2 m, and was available for a range of relatively deep-rooted crops in the following season. In this case the following crop had less soil mineral N available if a catch crop was grown. When the following crop was shallow-rooted, it was always an advantage to grow a catch crop.

- The root model was able to distribute root biomass and root length in different soil layers. Root distribution was determined by the exponential distribution, which not was in full agreement with field data for all dicot species, but was for most monocot species.

- This model setup shows the potential for N uptake from deeper soil layers, showing that the modelled distribution of root density was able to replicate field observations for mineral N.

7 Outlook

Papers I-III in this thesis describes different uses of models and different module compositions that can be considered in scenario simulations. Overall, this work demonstrates that it is possible to simulate root development and proliferation for a range of different crops and situations with a relatively simple root model approach with few parameters. Furthermore the results show the importance of better parameterisation of root modules in plant models for more accurate prediction of nitrate in the soil profile. For a better validation of root models, more experimental data are needed. There is still difficulty in using knowledge obtained in single root investigations in hydroponics or pot systems to understand the whole root system in the field.

Future work should focus on improving and developing more specific crop modules for grass-clover mixtures and intercropping of cereals and catch crops, in order to respond to the increased interest in modelling nitrate dynamics in complex crop rotation systems such as those studied here.

More knowledge is needed to understand root development and how plants search for water and nutrients. A possibility for further research for improving models could be an investigation of root development of transplanted crops. In vegetable production the use of transplants has increased and more vegetable species are now planted out instead of being grown from seed. For more accurate simulation and prediction of water and nitrogen demand in different soil layers (vertical and horizontal), more information is needed about crop development in the first three weeks after transplanting in order to analyse how the crop roots extend into the surrounding soil. Does the existing root continue growing out from the root block or do new roots develop from the meristem? Are there differences between dicot crops such as lettuce and cabbage compared with monocots such as onion and leek?

Further investigations of root depth, root distribution and nitrogen uptake from different soil layers will be also be an important step. It is important to know the rooting depth and root density/intensity at the root end for different crop species in order to complete a simulation for the whole crop rotation.

Another interesting issue for more detailed investigation is uptake of N from deeper layers when N is available in the surface layer. It is important in crop rotation planning and in model improvement to know whether crops with a deep rooting habit take up N from all soil layers, so that N losses to the environment can be minimised.

8 References

ABRAHAMSEN P & HANSEN S 2000. Daisy: an open soil-crop-atmosphere system model. Environmental Modelling and Software 15**,** 313-330.

ADIKU SGK, BRADDOCK RD & ROSE CW 1996. Modelling the effect of varying soil water on root growth dynamics of annual crops. Plant and Soil 185**,** 125-135.

ANONYMOUS 2000. Directive 2000/60/EC of the European parliament and of the council of 23 October 2000 establishing a framework for the Community action in the field of water policy. Official Journal of the European Communities L 327**,** 1-72.

AYLING SM 1993. The effect of ammonium ions on membrane potential and anion flux in roots of barley and tomato. Plant, Cell & Environment 16**,** 297-303.

BALDWIN JP 1975. A quantitative analysis of the factors affecting plant nutrient uptake from some soils. European Journal of Soil Science 26**,** 195-206.

BARBER SA 1984. Soil Nutrient Availability: A Mechanistic Approach. Wiley (Interscience), Toronto.

BARRACLOUGH PB 1984. The growth and activity of winter-wheat roots in the field - Root growth of high-yielding winter crops in relation to shoot growth. J.Agric.Sci. 103**,** 439-442.

BARRACLOUGH PB & LEIGH RA 1984. The growth and activity of winter wheat roots in the field: The effect of sowing date and soil type on root growth of high-yielding crops. Journal of Agricultural Science 103**,** 59-74.

BARRACLOUGH PB & WEIR AH 1988. Effects of a compacted subsoil layer on root and shoot growth, water-use and nutrition-uptake of winter-wheat. J.Agric.Sci. 110**,** 207-216.

BENGOUGH AG 1997. Modelling Rooting Depth and Soil Strength in a Drying Soil Profile. Journal of Theoretical Biology 186**,** 327-339.

BENGOUGH AG, BRANSBY MF, HANS J, MCKENNA SJ, ROBERTS TJ & VALENTINE TA 2006. Root responses to soil physical conditions; growth dynamics from field to cell. Journal of Experimental Botany 57**,** 437-447.

BERNTSEN J, GRANT R, OLESEN JE, KRISTENSEN IS, VINTHER FP, MOLGAARD JP & PETERSEN BM 2006a. Nitrogen cycling in organic farming systems with rotational grass-clover and arable crops. Soil Use and Management 22**,** 197-208.

BERNTSEN J, PETERSEN BM, JACOBSEN BH, OLESEN JE & HUTCHINGS NJ 2003. Evaluating nitrogen taxation scenarios using the dynamic whole farm simulation model FASSET. Agricultural Systems 76**,** 817-839.

BERNTSEN J, PETERSEN BM, OLESEN JE, ERIKSEN J & SØEGAARD K 2005. Simulation of residual effects and nitrate leaching after incorporation of different ley types. European Journal of Agronomy 23**,** 290-304.

BERNTSEN J, OLESEN JE, PETERSEN BM & HANSEN EM 2006b. Long-term fate of nitrogen uptake in catch crops. European Journal of Agronomy 25**,** 383-390.

BLOOM AJ, FRENSCH JUR & TAYLOR AR 2006. Influence of Inorganic Nitrogen and pH on the Elongation of Maize Seminal Roots. Annals of Botany 97**,** 867-873.

BORGESEN CD & SCHAAP MG 2005. Point and parameter pedotransfer functions for water retention predictions for Danish soils. Geoderma 127**,** 154-167.

BRADBURY NJ, WHITMORE AP, HART PBS & JENKINSON DS 1993. Modelling the fate of nitrogen in crop and soil in the yearsfollowing application of 15N-labelled fertilizer to winter wheat. J.Agric.Sci. 121**,** 363-379.

BRELAND TA 1996. Green manuring with clover and ryegrass catch crops undersown in small grains - effects on soil mineral nitrogen in field and laboratory experiments. Acta Agriculturae Scandinavica Section B - Soil and Plant Science 46**,** 178-185.

BREWSTER JL, BHAT KKS & NYE PH 1976. The possibility of predicting solute uptake and plant growth response from independently measured soil and plant characteristics. Plant and Soil 44**,** 295-328.

BRUUN S, CHRISTENSEN BT, HANSEN EM, MAGID J & JENSEN LS 2003. Calibration and validation of the soil organic matter dynamics of the Daisy model with data from the Askov long-term experiments. Soil Biology and Biochemistry 35**,** 67-76.

BUCKLAND ST, CAMPBELL CD, MACKIE-DAWSON LA, HORGAN GW & DUFF EI 1993. A method for counting roots observed in minirhizotrons and their theoretical conversion to root length density. Plant and Soil 153**,** 1-9.

BUSCOT F, MUNCH JC, CHARCOSSET JY, GARDES M, NEHLS U & HAMPP R 2000. Recent advances in exploring physiology and biodiversity of ectomycorrhizas highlight the functioning of these symbioses in ecosystems. FEMS Microbiology Reviews 24**,** 601-614.

CANNON WA 1949. A Tentative Classification of Root System. Ecology 30**,** 542-548.

CITOVSKY V & ZAMBRYSKI P 2000. Systemic transport of RNA in plants. Trends in Plant Science 5**,** 52-54.

CLARK LJ, WHALLEY WR, CLARK LJ, BARRACLOUGH PB & WHALLEY WR 2003. How do roots penetrate strong soil? Plant and Soil 255**,** 93-104.

CLARKE AL & BARLEY KP 1968. The uptake of nitrogen from soil in relations to solute diffusion. Australian Journal of Soil Research 6**,** 75-92.

COLEMAN K, JENKINSON DS, CROCKER GJ, GRACE PR, KLIR J, KORSCHENS M, POULTON PR & RICHTER DD 1997. Simulating trends in soil organic carbon in long-term experiments using RothC-26.3. Geoderma 81**,** 29-44.

CRAWFORD NM & GLASS ADM 1998. Molecular and physiological aspects of nitrate uptake in plants. Trends in Plant Science 3**,** 389-395.

DIGGLE AJ 1988. Rootmap: a root growth model. Mathematics and Computers in Simulation 30**,** 175-180.

DITOMASO J . Yellow startstle information. -15. 2001. University of California, Davis. http://wric.ucdavis.edu/yst.

DREW MC 1975. Comparison of the Effects of a Localized Supply of Phosphate, Nitrate, Ammonium and Potassium on the Growth of the Seminal Root System, and the Shoot, in Barley. New Phytologist 75**,** 479-490.

DUNBABIN V, DIGGLE A. & RENGEL Z 2003. Is there an optimal root architecture for nitrate capture in leaching environments. Plant Cell & Environment 26**,** 835-844.

DUNBABIN VM, DIGGLE AJ & RENGEL Z 2002. Simulation of field data by a basic three-dimensional model of interactive root growth. Plant and Soil 239**,** 39-55.

EL-NAGGAR A, EL-ARABY A, DE NEERGAARD A & HØGH-JENSEN H 2007. Crop responses to 15N-labelled organic and inorganic nitrogen sources. Nutrient Cycling in Agroecosystems.

ELERS B & HARTMANN HD 1987. Biologische Konservierung von Nitrat. Gemüse 4**,** 210-214.

EPHRATH JE, SILBERBUSH M & BERLINER PR 1999. Calibration of minirhizotron readings against root lensity data obtained from soil cores. Plant and Soil 209**,** 201-208.

ERIKSEN J 2001. Nitrate leaching and growth of cereal crops following cultivation of contrasting temporary grasslands. Journal of Agricultural Science 136**,** 271-281.

FAIVRE R, LEENHARDT D, VOLTZ M, BENOIT M, PAPY F, DEDIEU G & WALLACH D 2004. Spatialising crop models. Agronomie 24**,** 205-217.

FITTER AH & STICKLAND TR 1991. Architectural Analysis of Plant Root Systems. 2. Influence of Nutrient Supply on Architecture in Contrasting Plant Species. New Phytologist 118**,** 383-389.

FITTER AH, STICKLAND TR, HARVEY ML & WILSON GW 1991. Architectural Analysis of Plant Root Systems. 1. Architectural Correlates of Exploitation Efficiency. New Phytologist 118**,** 375-382.

FORDE BG 2002. Local and Long-Range Signaling Pathways Regulating Plant Responses to Nitrate. Annual Review of Plant Biology 53**,** 203-224.

FORDE BG & CLARKSON DT 1999. Nitrate and ammonium nutrition of plants: physiological and molecular perspectives. Advances in Botanical Research 30**,** 1-90.

GAHOONIA TS, CARE D & NIELSEN NE 1997. Root hairs and phosphorus acquisition of wheat and barley cultivars. Plant and Soil 191**,** 181-188.

GAHOONIA TS & NIELSEN NE 2004. Barley genotypes with long root hairs sustain high grain yields in low-P field. Plant and Soil 262**,** 55-62.

GASTAL F & LEMAIRA G 2002. N uptake and distribution in crops: an agronomical and ecophysiological perspective. Journal of Experimental Botany 53**,** 789-799.

GERWITZ A & PAGE ER 1974. Empirical Mathematical-Model to Describe Plant Root Systems. Journal of Applied Ecology 11**,** 773-781.

GLASS ADM & SIDDIQI MT 1995. Nitrogen absorption by plant roots. In: Nitrogen nutrition in higher plants., eds H Srivastava & R Singh, Associated Publishing Company, New Dehli, India pp 21-56.

GLINSKI J & LIPIEC J 1990. Soil physical condition and plant roots. CRC Press Inc. Baca Raton.

GRANATO TC & RAPER CD, JR. 1989. Proliferation of Maize (Zea mays L.) Roots in Response to Localized Supply of Nitrate. Journal of Experimental Botany 40**,** 263-275.

GREENWOOD DJ, GERWITZ A, STONE DA & BARNES A 1982. Root development of vegetable crops. Plant and Soil 68**,** 75-96.

GREENWOOD DJ, RAHN C, DRAYCOTT A, VAIDYANATHAN LV & PATERSON C 1996. Modelling and measurement of the effects of fertilizer-N and crop residue incorporation on N-dynamics in vegetable cropping. Soil Use & Management 12**,** 13-24.

GREENWOOD DJ, RAHN C, DRAYCOTT A, VAIDYANATHAN LV & PATERSON C 2001. Modelling N-response of field vegetable crops grown under diverse conditions with N_ABLE: A review. Journal of Plant Nutrition 24**,** 1799-1815.

GREGORY PJ 2006. Plant Root, Growth, function and interactions with the soil. Blackwell Scientific, Oxford.

GREGORY PJ & HINSINGER P 1999. New approaches to studying chemical and physical changes in the rhizosphere: an overview. Plant and Soil 211**,** 1-9.

HANSEN S, JENSEN HE, NIELSEN NE & SVENDSEN H . Daisy - soil plant atmostphere system model. A10. 1990. Ministry and the Environment, National Agency of Environmental Protection. Copenhagen. Technical Report.

HANSEN S, JENSEN HE, NIELSEN NE & SVENDSEN H 1991. Simulation of nitrogen dynamics and biomass production in winter wheat using the Danish simulation model daisy. Fertilizer Research 27**,** 245-259.

HEERAMAN DA & JUMA NG 1993. A Comparison of Minirhizotron, Core and Monolith Methods for Quantifying Barley (Hordeum vulgare L) and Fababean (Vicia faba L) Root Distribution. Plant and Soil 148**,** 29-41.

HENRIKSEN GH, BLOOM AJ & SPANSWICK RM 1990. Measurement of Net Fluxes of Ammonium and Nitrate at the Surface of Barley Roots Using Ion-Selective Microelectrodes. Plant Physiology 93**,** 271-280.

HINSINGER P, GOBRAN GR, GREGORY PJ & WENZEL WW 2005. Rhizosphere geometry and heterogeneity arising from root-mediated physical and chemical processes. New Phytologist 168**,** 293-303.

HO MD, MCCANNON BC & LYNCH JP 2004. Optimization modeling of plant root architecture for water and phosphorus acquisition. Journal of Theoretical Biology 226**,** 331-340.

HODGE A, BINSON D, IFFITHS BS & ITTER AH 1999. Why plants bother: root proliferation results in increased nitrogen capture from an organic patch when two grasses compete. Plant, Cell and Environment 22**,** 811-820.

JENKINSON DS & RAYNER JH 1977. The turnover of soil organic matter in some of the Rothamsted classical experiments. Soil Science 123**,** 298-305.

JOHNSON JW & WILKENSON RE 1992. Wheat growth-responses of cultivars to H^+ concentration. Plant and Soil 146**,** 55-59.

JORDAN WR & MILLER FR 1980. Genetic variability in sorghum root systems: implication for drought tolerance. In: Adaptation of Plants to Water and High Temperature Stress, Wiley Interscience, New York pp 383-400.

JORDAN WR & MONK RL 1982. Enhancement of drought resistance in sorghum: progress and limitations. In: Proc. 35th Annu. Corn and Sorghum Res. Conf., pp 185-191.

JUNGK A 1991. Dynamics of nutrient movement at the soil-root interface. In: Plant Roots, The Hiden Half, eds J Waisel, A Eshel, & U Kafkafi, Marcel Dekker, New York pp 455-481.

KAGE H 1997. Is low rooting density of faba beans a cause of high residual nitrate content of soil at harvest? Plant and Soil 190**,** 47-60.

KAGE H, KOCHLER K & STÜTZEL H 2000. Root growth of cauliflower (Brassica oleracea L. botrytis) under unstressed conditions: Measurement and modelling. Plant and Soil 223**,** 133-147.

KASPAR TC & BLAND WL 1992. Soil temperature and root growth. Soil Science 154**,** 290-299.

KIRKEGAARD JA, LILLEY JM, HOWE GN & GRAHAM JM 2007. Impact of subsoil water use on wheat yield. Australian Journal of Agricultural Research 58**,** 303-315.

KRISTENSEN HL & THORUP-KRISTENSEN K 2004. Root Growth and Nitrate Uptake of Three Different Catch Crops in Deep Soil Layers. Soil Science Society of America Journal 68**,** 529-537.

LAZOF DB, RUFTY TW, JR. & REDINBAUGH MG 1992. Localization of Nitrate Absorption and Translocation within Morphological Regions of the Corn Root. Plant Physiology 100**,** 1251-1258.

LEY GJ, MULLINS CE & LAL R 1989. Hard-setting behaviour of some structurally weak tropical soils. Soil and Tillage Research 13**,** 365-381.

LIU KH, HUANG CY & TSAY YF 1999. CHL1 Is a Dual-Affinity Nitrate Transporter of Arabidopsis Involved in Multiple Phases of Nitrate Uptake. THE PLANT CELL 11**,** 865-874.

LUDEWIG U, VON WIREN N & FROMMER WB 2002. Uniport of NH4+ by the Root Hair Plasma Membrane Ammonium Transporter LeAMT1;1. Journal of Biological Chemistry 277**,** 13548-13555.

LYNCH JP 1995. Root Architecture and Plant Productivity. Plant Physiology 109**,** 7-13.

LYNCH JP, NIELSEN KL, DAVIS RD & JABLOKOW AB 2007. SimRoot: Modeling and visualization of botanical root systems. Plant and Soil 139-151.

MACDUFF J & WILD DA 1989. Interactions between Root Temperature and Nitrogen Deficiency Influence Preferential Uptake of NH+4 and NO-3 by Oilseed Rape. Journal of Experimental Botany 40**,** 195-206.

MADSEN HB 1985. Distribution of spring barley roots in Danish soils of different texture and under different climatic conditions. Plant and Soil 88**,** 31-43.

MARSCHNER H 1995. Mineral Nutrition of higher plants. Acadimic Press, London.

MARSCHNER H 1998. Role of root growth, arbuscular mycorrhiza, and root exudates for the efficiency in nutrient acquisition. Field Crops Research 56**,** 203-207.

MATERECHERA SA, DEXTER AR & ALSTON AM 1991. Penetration of very strong soils by seedling roots of different plant species. Plant and Soil V135**,** 31-41.

MCCLURE PR, KOCHIAN LV, SPANSWICK RM & SHAFF JE 1990. Evidence for Cotransport of Nitrate and Protons in Maize Roots : I. Effects of Nitrate on the Membrane Potential. Plant Physiology 93**,** 281-289.

MCMICHAEL BL & BURKE JJ 1998. Soil temperature and root growth. Hortscience 33**,** 947-951.

MERRILL SD & UPCHURCH DR 1994. Converting root numbers observed at minirhizotrons to equivalent root length density. Soil Science Society of America Journal 58**,** 1061-1067.

MILLER A & CRAMER M 2005. Root Nitrogen Acquisition and Assimilation. Plant and Soil 274**,** 1-36.

MILLER AJ & SMITH SJ 1996. Nitrate transport and compartmentation in cereal root cells. Journal of Experimental Botany 47**,** 843-854.

MILLER RH & SCHMIDT EL 1965. Uptake and assimilation of amino acids supplied to the sterile soil: root environment of the bean plant (Phaseolus vulgaris). Soil Science 100**,** 323-330.

NACRY P, CANIVENC G, MULLER B, AZMI A, VAN ONCKELEN H, ROSSIGNOL M & DOUMAS P 2005. A Role for Auxin Redistribution in the Responses of the Root System Architecture to Phosphate Starvation in Arabidopsis. Plant Physiology 138**,** 2061-2074.

NAZOA P, VIDMAR JJ, TRANBARGER TJ, MOULINE K, DAMIANI I, TILLARD P, ZHUO D, GLASS ADM & TOURAINE B 2003. Regulation of the nitrate transporter gene AtNRT2.1 in Arabidopsis thaliana: responses to nitrate, amino acids and developmental stage. Plant Molecular Biology 52**,** 689-703.

NEWMANN EI 1966. A method of estimating the total length of root in a sample. Journal of Applied Ecology 11**,** 309-314.

NIELSEN NE & BARBER SA 1978. Diffferences Among Genotypes of Corn in the Kinitics of P Uptake. Agronomy Journal 70**,** 695-698.

OADES JM & WATERS AG 1991. Aggregate hierarchy in soils. Australian Journal of Soil Research 29**,** 815-828.

OWEN AG & JONES DL 2001. Competition for amino acids between wheat roots and rhizosphere microorganisms and the role of amino acids in plant N acquisition. Soil Biology and Biochemistry 33**,** 651-657.

PAGES L & PELLERIN S 1996. Study of differences between vertical root maps observed in a maize crop and simulated maps obtained using a model for the three-dimensional architecture of the root system. Plant and Soil 182**,** 329-337.

PAGES L, VERCAMBRE G, DROUET J-L, LECCOMPTE F, COLLET C & LE BOT J 2004. Root Typ: a generic model to depict and analyse the root system architecture. Plant and Soil 258**,** 103-119.

PARTON WJ, SCHIMEL DS, COLE CV & OJIMA DS 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. Soil Science Society of America Journal 51**,** 1173-1179.

PEDERSEN A, JENSEN LS & THORUP-KRISTENSEN K 2005. A model analysis on nitrate leaching under different soil and climate conditions and use of catch crops. Poster presented at 14th N Workshop "N management in agrosystems in relation to the Water Framework Directive" Held 24-26 October 2005, Maastricht, The Netherlands.

PERSSON J & NASHOLM T 2001. Amino acid uptake: a widespread ability among boreal forest plants. Ecology Letters 4**,** 434-438.

PETERSEN BM, BERTNSEN J, HANSEN S & JENSEN LS 2005a. CN-SIM - a model for the turnover of soil organic matter. I: Long-term carbon and radiocarbon development. Soil Biology and Biochemistry 37**,** 359-374.

PETERSEN BM, JENSEN LS, HANSEN S, PEDERSEN A, HENRIKSEN TM, SØRENSEN P, TRINSOUTROT-GATTIN I & BERNTSEN J 2005b. CN-SIM - a model for the turnover of soil organic matter. II: Short-term carbon and nitrogen development. Soil Biology and Biochemistry 37**,** 375-393.

PIERRET A, MORAN CJ & DOUSSAN C 2005. Conventional detection methodology is limiting our ability to understand the roles and functions of fine roots. New Phytologist 166**,** 967-980.

PREGITZER KS 2002. Fine roots of trees - a new perspective. New Phytologist 154**,** 267-270.

RICKMAN RW, KLEPPER B & BALL DA 1995. An algorithm for predicting crown root axes of annual grasses. Agronomy Journal 87**,** 1182-1186.

ROBINSON D 1996. Resource Capture by Localized Root Proliferation: Why Do Plants Bother? Annals of Botany 77**,** 179-186.

ROBINSON D 2001. Root proliferation, nitrate inflow and their carbon costs during nitrogen capture by competing plants in patchy soil. Plant and Soil 232**,** 41-50.

ROBINSON D, LINEHAN DJ & CAUL S 1991. What limits nitrate uptake from soil? Plant, Cell & Environment 14**,** 77-85.

ROBINSON D, LINEHAN DJ & GORDON DC 1994. Capture of nitrate from soil by wheat in relation to root length, nitrogen inflow and availability. New Phytologist 128**,** 297-305.

ROSE DA 1983. The description of the growth of root systems. Plant and Soil 75**,** 405-415.

ROSOLEM CA, FOLONI JSS & TIRITAN CS 2002. Root growth and nutrient accumulation in cover crops as affected by soil compaction. Soil and Tillage Research 65**,** 109-115.

RYKIEL EL 1996. Testing ecological models: The meaning of validation. Ecological Modelling 90**,** 229-244.

SAMSON BK & SINCLAIR TR 1994. Soil core and minirhizotron comparison for the determination of root length density. Plant and Soil 161**,** 225-232.

SANDERS D, HANSEN UP, GRADMANN D & SLAYMAN CL 1984. Generalized kinetic analysis of ion-driven co-transport systems:a unified interpretation of sleetive ionic effects on Michaelis-Menten parameters. J.Membr.Biol. 77**,** 123-152.

SCHENK JH & JACKSON EB 2002. Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. Journal of Ecology 90**,** 480-494.

SINGH BP & SAINJU UM 1998. Soil physical and morphological properties and root growth. Hortscience 33**,** 966-971.

SMITH JU, BRADBURY NJ & ADDISCOTT TM 1996. SUNDIAL: A PC-based system for simulating nitrogen dynamics in arable land. Agronomy Journal 88**,** 43.

STIRZAKER RJ, PASSIOURA JB & WILMS Y 1996. Soil structure and plant growth: impact of bulk density and biopores. Plant and Soil 185**,** 151-162.

TAYLOR AR & BLOOM AJ 1998. Ammonium, nitrate, and proton fluxes along the maize root. Plant, Cell & Environment 21**,** 1255-1263.

TAYLOR HM, UPCHURCH DR & MCMICHAEL BL 1990. Applications and limitations of rhizotrons and minirhizotrons for root studies. Plant and Soil 129**,** 29-35.

TENNANT D 1975. A test of a modified line intersect method of estimating root length. Journal of Ecology 63**,** 995-1001.

THORUP-KRISTENSEN K, MAGID J & JENSEN LS 2003. Catch crops and green manures as biological tools in nitrogen management in temperate zones. In: Advances in Agronomy, ed Sparks, Academic Press, pp 227-302.

THORUP-KRISTENSEN K 2001. Are differences in root growth of nitrogen catch crops important for their ability to reduce soil nitrate-N content, and how can this be measured? Plant and Soil 230**,** 185-195.

THORUP-KRISTENSEN K 2006. Effect of deep and shallow root systems on the dynamics of soil inorganic N during 3-year crop rotations. Plant and Soil 288**,** 233-248.

TILLARD P, PASSAMA L & GOJON A 1998. Are phloem amino acids involved in the shoot to root control of NO3- uptake in Ricinus communis plants? Journal of Experimental Botany 49**,** 1371-1379.

VAN WIJK WR 1963. Physiscs of plant enviroment. North-Holland publ. Co., Amsterdam.

VANCE CP 2002. Root-bacteria interactions. Symbiotic Nitrogen fixation. In: Plant roots: The hidden half, eds Y Waisel, A Eshel, & U Kafkafi, Marcel Dekker, New York pp 839-868.

VOS J & VAN DER PUTTEN PEL 1997. Field observations on nitrogen catch crops. I. Potential and actual growth and nitrogen accumulation in relation to sowing date and crop species. Plant and Soil 195**,** 299-309.

WALCH-LIU PIA, IVANOV II, FILLEUR SOPH, GAN Y & REMANS T 2006. Nitrogen Regulation of Root Branching. Annals of Botany 97**,** 875-881.

WILLIAMSON LC, RIBRIOUX SPCP, FITTER AH & LEYSER HMO 2001. Phosphate Availability Regulates Root System Architecture in Arabidopsis. Plant Physiology 126**,** 875-882.

WRAITH JM & WRIGHT CK 1998. Soil water and root growth. Hortscience 33**,** 951-959.

WU L, MCGECHAN MB, MCROBERTS N, BADDELEY JA & WATSON CA 2007. SPACSYS: Integration of a 3D root architecture component to carbon, nitrogen and water cycling - Model description. Ecological Modelling 200**,** 343-359.

ZHANG H & FORDE BG 1998. An Arabidopsis MADS box gene that controls nutrient-induced changes in root architecture. Science 279**,** 407-409.

ZHANG H, JENNINGS A, BARLOW PW & FORDE BG 1999. Dual pathways for regulation of root branching by nitrate. Proceedings of the National Academy of Sciences 96**,** 6529-6534.

ZHANG H & FORDE BG 2000. Regulation of Arabidopsis root development by nitrate availability. Journal of Experimental Botany 51**,** 51-59.

ZOBEL R 2003. Fine roots - discarding flawed assumptions. New Phytologist 160**,** 276-279.

Paper I:

Anders Pedersen, Bjørn M. Petersen, Jørgen Eriksen, Søren Hansen and Lars Stoumann Jensen 2007. A model simulation analysis of soil nitrate concentrations – does soil organic matter pool structure or catch crop growth parameters matter most? *Ecological Modelling* 205:1-2, 209-220.

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Simulating nitrate retention in soils and the effect of catch crop use and rooting pattern

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Keywords: Nitrate retention, catch crop, nitrogen use efficiency, rooting depth
Short running head title: Simulating nitrate retention in soils

Abstract

This model analysis of catch crop effects on nitrate retention covered three soil texture classes (sand, loamy sand, sandy loam) and three precipitation regimes (557, 627 and 850 mm, Aug-May) in a temperate climate representative for Denmark. Each of the three climate regimes included 43 years of weather data. Simulations were made with two catch crops (ryegrass and *Brassica*) with different rooting depths, and soil N effects in the next spring were analysed to 0.25, 0.75 and 2.0 m depth to represent the catch crop effect on following crops with different rooting depths. The retained nitrate fraction was generally located in deeper soil layers. In the low precipitation regime the overall fraction of nitrate retained in the 0-2.0 m soil profile was 0.23 for the sandy soil, 0.69 for the loamy sand and 0.81 for the sandy loam (median values).

Ryegrass reduced leaching losses much less efficiently than *Brassica*. *Brassica* depleted the 0-0.75 m soil layer of nitrate more completely than ryegrass and furthermore depleted some nitrate in the deeper soil layer, which the ryegrass could not reach. A positive N effect (N_{eff}, mineral N content after catch crop compared with mineral N content after bare soil) was found in the 0-0.25 m layer in all three soil texture classes, with on average 10 kg N ha^{-1} for ryegrass and 34 kg N ha^{-1} for *Brassica*. In the whole soil profile (0-2.0 m), a positive N_{eff} was only found in the sandy soil, whereas a mainly negative N_{eff} was found in the loamy sand and especially the sandy loam. The simulations showed that for shallow-rooted N_{eff} values were always positive, whereas N_{eff} for deeper-rooted crops depended strongly on soil and weather conditions. It was positive under high-leaching conditions such as sandy soils with high precipitation, whereas on more retentive soils and with less precipitation it tended to be negative.

Keywords: Nitrate retention, catch crop, nitrogen use efficiency, rooting depth

Introduction

Climatic and soil textural conditions in intensive crop production areas can influence nitrate losses to the surrounding environment. This may cause nitrate concentrations in drinking water to exceed the EU Drinking Water Directive upper limit of 50 mg L^{-1} nitrate (Anonymous, 2000). To comply with the EU Drinking Water Directive, the Danish government has implemented a number of action plans for the aquatic environment, the latest from 2004. Part of this action plan has been to set up regulations for fertiliser application and mandatory use of catch crops to minimise mineral N losses.

Denmark has a temperate coastal climate characterised by relatively mild winters and surplus precipitation in the winter. The distribution of precipitation varies widely between regions, the maximum in central and south-western Jutland with above 900 mm y^{-1} and the minimum in coastal areas of Sealand with below 500 mm y^{-1} (Frich *et al*., 1997). The extension of the ice cover during the last ice age has resulted in a gradient in soil texture distribution across the country, with sandy soils from glacial outwash in western Jutland to sandy clay loams from the Weichselian moraine in the remainder of the country. The sandy soils with low water-holding capacity therefore generally occur in the areas with high precipitation, and the more loamy soils in areas with lower precipitation. This leads to rather different situations of nitrate leaching risk, requiring different choices of crop and catch crop strategies to avoid nitrate leaching below the rooting zone (Vos *et al*., 1998; Askegaard *et al*., 2005).

The conditions for crop growth and development are often not optimal in autumn after harvest, with shorter day length, low radiation, dry conditions, low temperature and large variation in availability of mineral N in the soil profile. Typical catch crops are undersown ryegrasses or cruciferous species sown before or immediately after harvest in cereals. Under optimal conditions a catch crop can take up 3-4 kg N ha^{-1} day^{-1}, hold 3-4% N in its dry matter and empty the soil of mineral N in a few weeks of active growth (Vos and van der Putten, 1997). Good establishment is important for

optimal catch crop growth. Crucifers are more sensitive to the date of sowing in autumn than monocot species (Elers and Hartmann, 1987; Vos and van der Putten, 1997). However, crucifers have a higher root penetration rate and rooting depth, which means that they are normally able to reach nitrate before excess precipitation transports it further down, or to reach nitrate left in deeper soil layers (Thorup-Kristensen, 2001; Kristensen and Thorup-Kristensen, 2004).

Ryegrass is winter-hardy in temperate climates, whereas some cruciferous species die off during winter. This is an advantage when ryegrass is grown as a catch crop in sandy soil in areas with high winter and spring precipitation, because *Brassica* may release N from decomposed plant residues too early. However, using winter-hardy catch crops that are incorporated just before a spring crop can result in pre-emptive competition, because they take up N from the rooting zone of the succeeding crop (Willumsen and Thorup-Kristensen, 2001). Winter surplus of precipitation, soil water-holding capacity and root depth of the succeeding crop determine the nitrate movement and the magnitude of this pre-emptive effect. When root depth of the following crop is shallow (e.g. 0.25 m or 0.5 m), both ryegrass and *Brassica* catch crops normally have a positive effect on the amount of available N. However if the main crop has a rooting depth of 1.0 m or more, a ryegrass catch crop can have a negative effect on available N in climate zones with low precipitation and soils with high water-holding capacity, because this crop is able to take up N from the same soil layers. On the other hand, in situations where the catch crop has a deeper root system than the following main crop, the catch crop will be able to retain N at depths below the rooting zone of the following crop, which will have a positive effect on the overall nitrogen balance for a number of years.

To evaluate the effect of soil texture and climate conditions in different situations with and without catch crops, it is an advantage to use soil-plant models. A commonly used model is the soil-plant-atmosphere model Daisy, which has been extensively used and validated for modelling N turnover

and N leaching in crop rotations (de Willigen, 1991; Diekkrüger *et al*., 1995; Mueller *et al*., 2006). The model can be characterised as a dynamic, deterministic and semi-mechanistic agro-ecosystem model (Abrahamsen and Hansen, 2000; Hansen *et al*., 1991)

The aim of the present study was to analyse the effect of catch crop use and rooting depth on nitrate retention as affected by precipitation and soil texture under Danish conditions. This was done by developing a set of one-year simulations covering different soil types, precipitation regimes and catch crops, with climatic input data covering a period of 43 years. The simulations were made using the Daisy model. The results were used to analyse: i) Nitrate retention in soils of different textural properties when subjected to different precipitation regimes and without catch crops; ii) the effect of catch crops with different rooting patterns on nitrate availability and depth distribution in the following spring; iii) nitrate retention without catch crops compared with catch crop effect on soil N in the following spring; and iv) effect of root depth of the following main crop on the conclusions.

Materials and methods

Simulations

Table 1 shows a schematic overview of the simulation analyses of three different soil types and three different climate regimes. The soil types were sandy soil (24% of Danish arable land), loamy sand soil (21% of Danish arable land) and sandy loam (20% of Danish arable land). For soil textural properties, see below. The climate regimes were low, medium and high precipitation regimes (see details below). The simulations started each year on 1 June and ended on 1 May in the following year. To examine the effects of precipitation regime and catch crops on nitrate retention, simulations with and without catch crops were tested. The first simulation analysed nitrate retention in soils without catch crops. Here two levels of nitrate were added in a bare soil simulation: 20 kg N ha^{-1} in the 0-0.25 m layer and 20 kg N ha^{-1} in the 0.25-1.00 m layer (40 kg applied nitrate-N ha^{-1}); or 25 kg N ha^{-1} in the 0-0.25 m layer and 25 kg N ha^{-1} in the 0.25-1.00 m layer (50 kg applied nitrate-N ha^{-1}). Nitrate was added on 15 August in both simulations.

Table 1. Overview of the two simulation series analysed. Simulations include three precipitation regimes and three soil types. Simulations start 1 June, end 1 May. Nitrate retention simulation includes two bare soil treatments, while catch crop simulation includes two bare soil and two catch crops treatments. Nitrate application 15 August. Catch crops sown 15 August, incorporated 1 December

Main factors		**Simulation 1**	**Simulation 2**
Precipitation regime	**Soil types**	**Analysing nitrate retention in bare soil**	**Analysing the effect of catch crop use**
Low	Sandy soil	Bare soil (40 kg mineral N ha^{-1})	Bare soil (0 kg mineral N ha^{-1})
Medium	Loamy sand soil	Bare soil (50 kg mineral N ha^{-1})	Bare soil (50 kg mineral N ha^{-1})
High	Sandy loam		Ryegrass (50 kg mineral N ha^{-1})
			Brassica (50 kg mineral N ha^{-1})

The second simulation analysed the use of two catch crops, ryegrass and *Brassica* (spring rape), sown on 15 August and incorporated into soil on 1 December. To represent N from the preceding crop, 25 kg ha^{-1} of nitrate-N was added in the 0-0.25 m layer and a further 25 kg N ha^{-1} in the 0.25-1.00 m layer (50 kg applied nitrate-N ha^{-1}). A further treatment with no catch crop and no

application of nitrate was used and application of 50 kg nitrate-N ha^{-1} from first simulation was included. Date of catch crop sowing and incorporation was tested by simulating ryegrass and *Brassica* sowing on 15 July, 1 and 15 August and 1 September, and biomass incorporation on 1 October, 1 November, 1 December, 1 January, 1 February, 1 March and 1 April. All combinations of soil type, climate regime, catch crop use, sowing dates and incorporation date were simulated, giving rise to 864 different combinations which were simulated for 43 years with natural variations in climate. From these, only one sowing date (15 August) and one incorporation date (1 December) were selected for the purposes of the current study, as only small and insignificant effects were found for all other sowing dates and 1 Dec was considered the most relevant incorporation date.

Daisy Model Simulations

The current simulations were carried out with version 4.0 of the Daisy model (Abrahamsen and Hansen, 2000). Physical and hydraulic parameters for soil horizons were taken from default settings for sand soil (clay 3.9%, sand 87%, WHC (pF 2.00) 0-0.2 m 12.4%v/v, 0.2-2.5 m 8% v/v); loamy sand soil (clay 7.9%, sand 68%, WHC (pF 2.00) 0-0.2 m 20.0%v/v, 0.2-2.5 m 15.3% v/v) and sandy loam (clay 12.4% sand 60%, WHC (pF 2.00) 0-2.0 m 21.3%v/v, 0.2-2.5 m 19% v/v) (after USDA system). Soil types are initiated by default settings for the SOM sub-module. Nitrate and ammonia content at the start of simulation was according to default setup of soil types and organic matter module.

Climate and weather

Effects of different climate conditions were studied by modifying weather data from Aarslev Research Centre in the period 1960-2003. Real weather data for this location (except precipitation amount) were used in all simulations. Three different precipitation regimes were constructed to represent regions in Denmark. These were taken from the counties of West Zealand, Fynen and

Ribe (West Jutland) (Frich *et al*., 1997), representing a low, medium and high precipitation regime in Denmark. The average precipitation for each month over the period 1961-1990 was used to calculate monthly scaling coefficients for construction of the precipitation regime. Precipitation data were then scaled for measurement error according to Allerup *et al*. (1998) and wet and dry atmospheric N deposition was set according to Ellerman *et al*. (2002). Average monthly precipitation for the three regimes is shown in Table 2, together with cumulative values for minimum, average and maximum precipitation from the date of mineral N application to 1 May. In order to determine the effect of climatic variation, each simulation was performed using weather data from all years from 1960 to 2003.

Table 2. Average surface-corrected precipitation (ppn.) each month (mm) in the low, medium and high precipitation regimes (Frich *et al*., 1997) and medium, minimum and maximum precipitation (mm) in the simulation period 15 August - 1 May

Regime	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Annual	15 August- 1 May		
														Medium	Min.	Max
Low ppn.	65	43	51	45	49	54	67	65	62	63	71	74	**709**	557	196	788
Medium ppn.	78	53	58	48	52	59	69	69	71	72	82	84	**796**	627	222	896
High ppn.	96	61	73	56	57	69	75	88	99	114	125	114	**1026**	850	302	1206

Catch crops

For ryegrass, the default Daisy crop model for grass was used, while for *Brassica* the Daisy crop module for spring rape was used. The main difference in parameterisation of the two crop modules is that *Brassica* has a faster rate of development in the vegetative phase, faster root penetration rate, a higher potential N% in leaves late in the vegetative phase and early reproductive phase (6% compared with 3% for ryegrass) and potential root depth is calculated to be 0.7 m for ryegrass and 2.5 m for *Brassica* according to field data (Thorup-Kristensen, 2001; Thorup-Kristensen, 2006b).

Data analysis

Rooting depth of the following main crop determines the depth to which the residual N can be recovered by this crop. We introduced three root depth categories, namely 0.25 m as shallow, 0.75 m as medium and 2 m as deep-rooted main crops. We then analysed the amount of mineral N present down to these depths on 1 May, when the following crop should be well-established.

The simulations were divided into two sets, bare soil simulations and simulations with a comparison of bare soil with the two different catch crops. In bare soil simulations, the fraction of residual mineral N retained to a given soil depth was calculated by subtracting the amount of mineral N to that depth on 1 May in the simulation with 40 kg applied nitrate-N from the amount of mineral N in the simulation with 50 kg applied nitrate-N and dividing by the 10 kg nitrate-N difference from the beginning of the simulation period. In this simulation setup, there was no difference in N mineralisation, immobilisation or denitrification; therefore the only possible 'sink' for soil mineral N is nitrate transported together with soil water percolation. In the second simulation, 25 kg mineral N ha^{-1} were added to both the 0-0.25 m layer and the 0.25-1.0 m layer on the day of sowing of catch crops to simulate a residual mineral N content after a main crop that had not efficiently emptied the soil profile of N. Two bare soil simulations were carried out to compare with catch crop simulations; one without addition of nitrate N and one with the same amount of nitrate N as in the catch crop simulations.

Results

Retention of nitrate in bare soil

Precipitation regime had a large influence on bare soil nitrate retention in the selected soil types. The average nitrate retention in the whole soil profile (0-2.0 m) with the high and low precipitation regimes was 0.09 and 0.41 respectively for the sandy soil, 0.32 and 0.76 for the loamy sand soil and 0.47 to 0.84 for the sandy loam (Figure 1).

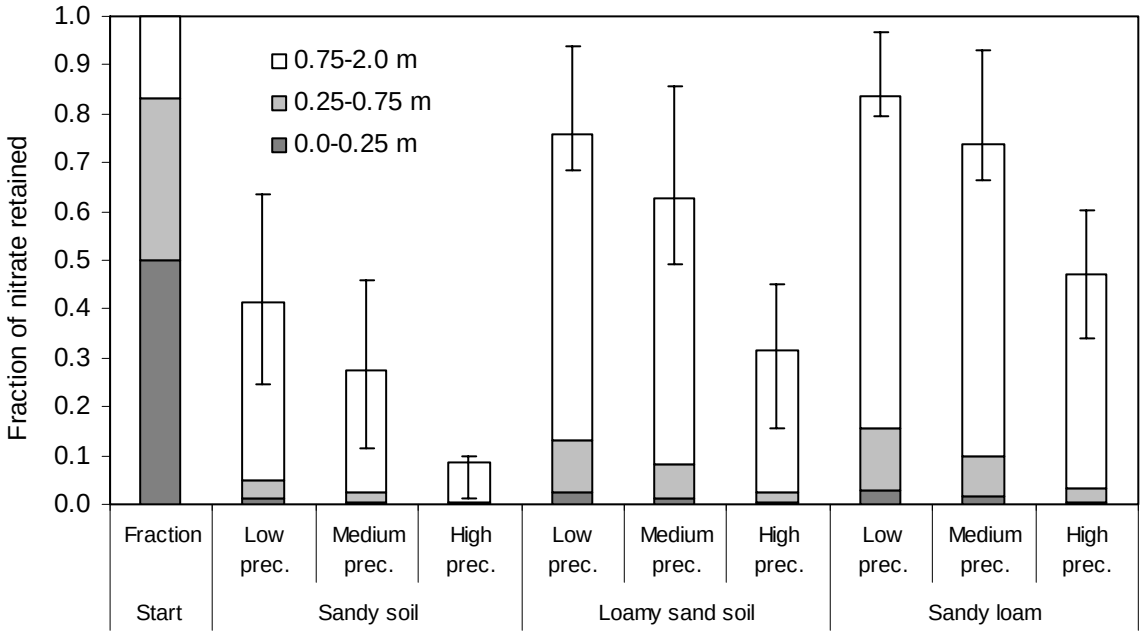

Figure 1. Distribution of nitrate added on 15 Aug and average fractions of mineral N retained on 1 May in bare soil simulations. Data for three soil layers, three soil types and three precipitation regimes. The bars show the 25 and 75% percentiles over 43 years simulated for a 0-2.0 m soil profile.

Average nitrate retention was low in the 0-0.25 m layer for all simulations, with a retained fraction from below 0.01 to 0.03 (Figure 1). In the 0.25-0.75 m layer, the sandy soil still had a low nitrate retention, with a fraction of only up to 0.05, whereas the loamy sand and sandy loam soils with their higher water-holding capacity could retain a fraction of on average 0.13 and 0.16, respectively, of the residual nitrate (Figure 1). In the 0.75-2.0 m layer the retention was higher, varying from a fraction of 0.1 on sandy soils up to a fraction of 0.65 on both loamy sand and sandy loam.

In sandy soils receiving high precipitation, nitrate from the topsoil was leached out at 2.0 m depth (Figure 2). Loamy sand and sandy loam showed higher retention and for medium and low precipitation regimes, the nitrate leaching front only reached a depth of 1.25 and 1.75 m respectively (Figure 2). In the high precipitation regime, 96% of the simulated years showed retention of less than 0.2 in the 0-2.0 m sandy soil profile (Figure 3), but in the low precipitation regime 25% of the simulated years showed retention above 0.5. Loamy sand soil and sandy loam, which had higher soil water-holding capacity than the sandy soil, showed higher retention, only below 0.6 for sandy loam and 0.5 for loamy sand in 8% of the simulated years with the low precipitation regime (Figure 3).

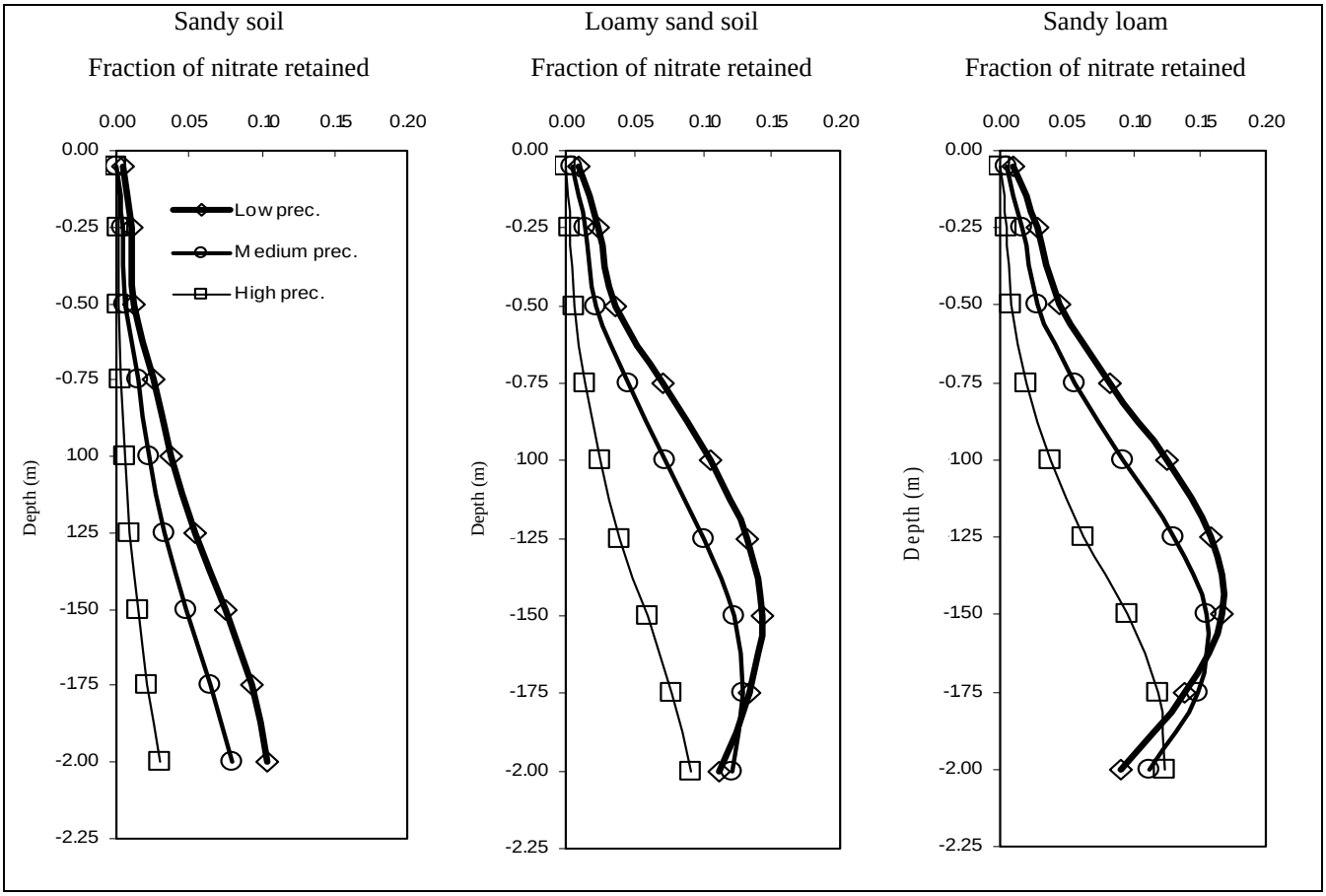

Figure 2. Simulated distribution of residual mineral N fraction retained with depth on 1 May in bare soil simulations for a 0-2.0 m soil profile for three soil types and three precipitation regimes. Points show retention within each 0.25 m layer.

Although precipitation regime had a large effect on retention, there was an even larger variation between years within each precipitation regime. Figure 3 shows the variation in nitrate retention using data for the single simulated years. In the high precipitation regime, precipitation differed from 1206 mm in the wettest autumn/winter to 302 mm in the driest (Table 2), resulting in a nitrate retention fraction in these specific years of 0.01 and 0.88 respectively on sandy soil and 0.01 and 0.99 respectively on both loamy sand soil and sandy loam. The nitrate retention showed a normal variation between most of the years, except for four seasons out of the 43 seasons when the precipitation was very high and little nitrate was retained even in the sandy loam soil, and two seasons when the precipitation was so low that a high fraction of the nitrate was retained even in the sandy soil simulations (Figure 3).

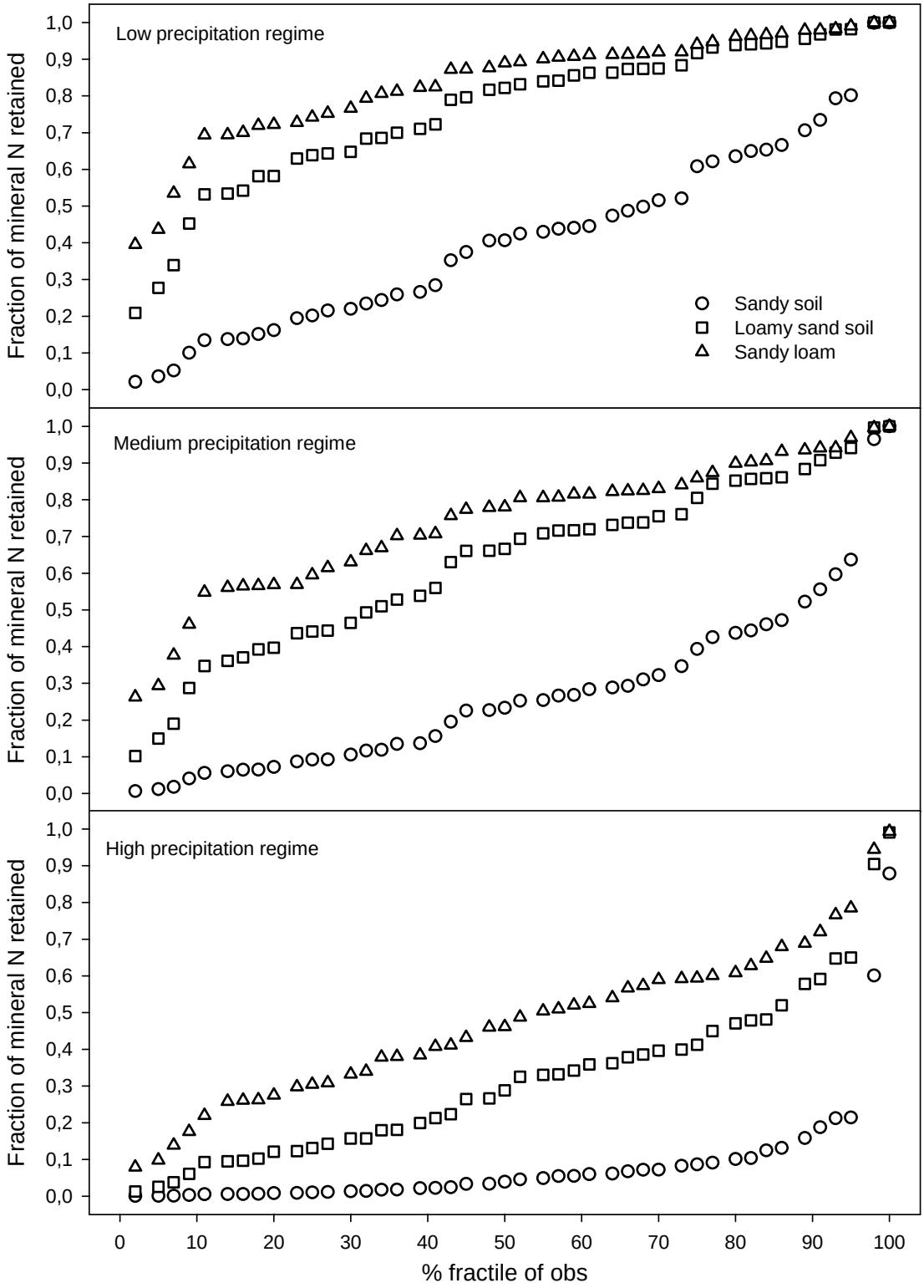

Figure 3. Fractile distribution of the between-year variation in fraction of mineral N retained in the 0-2.0 m soil profile on 1 May in bare soil. Simulations with climate data from 43 years and either low, medium or high precipitation regime. Key to symbols within diagram.

Catch crop simulations

The use of catch crops had a high impact on mineral N distribution in the soil layers and on nitrate leaching (Figure 4). Mean catch crop N uptake from the soil was 65 kg N ha^{-1} for ryegrass (limited rooting depth) and 92 kg N ha^{-1} for *Brassica* (deep rooting) by 1 December.

Figure 4a shows average mineral N content in the soil on 1 Dec, the day when the catch crops were incorporated. On this date, soil nitrate content in the sandy soil (50 kg N added) with or without catch crop was only 5 to 8 kg N ha^{-1} in the upper layer (0-0.25 m), due to leaching and plant uptake where catch crops were grown. However, in the 0.25-0.75 m soil layer the sandy soil contained 20, 6 and 3 kg N ha^{-1} with bare soil, ryegrass and *Brassica*, respectively, clearly indicating that both catch crop species took up soil mineral N from this layer, and that the deep-rooted catch crop was more effective. The deeper subsoil (0.75-2.0 m) contained 68, 35 and 14 kg N ha^{-1} with bare soil, ryegrass and *Brassica*, respectively (Figure 4b), showing even larger effects of catch crops and of differences in rooting depth between the two types of catch crop.

Growing a deep-rooted catch crop reduced nitrate leaching more efficiently than growing a medium-rooted catch crop (Figure 5), with average leaching losses to below 2.0 m of 16 and 34 kg N ha^{-1} for the two catch crops (data not shown). Furthermore, the importance of growing a catch crop and the significance of catch crop rooting depth for nitrate leaching to below 2.0 m increased from the sandy loam soil to the sandy soil with much lower water-holding capacity.

The catch crop influences the water balance through increased evapotranspiration, which may in turn affect soil water percolation and hence leaching. However, for simulations without a catch crop, average transpiration was 326 mm y^{-1}, compared with total evapotranspiration of 341 and 345 mm y^{-1} for the ryegrass and *Brassica* simulations respectively, indicating that the catch crops affected soil water percolation minimally.

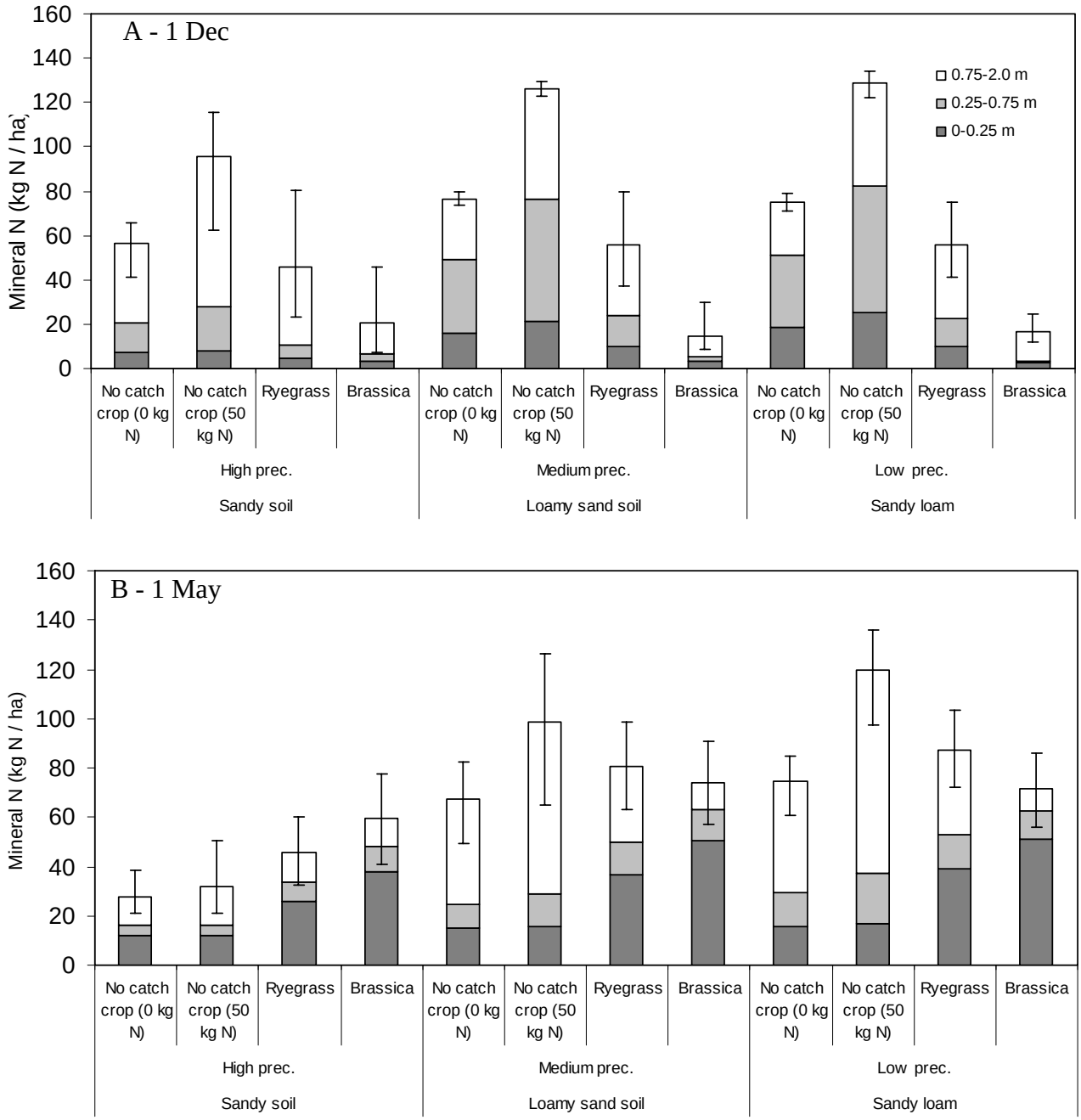

Figure 4. Simulated average values of mineral N content in three soil layers on a) 1 Dec. and b) 1 May for bare soil without application and with application of 50 (kg N ha^{-1}) and two different catch crops in three different soil and climate regimes. The figure illustrates simulated variations in low, medium and high nitrate retention in different precipitation and soil combinations. Bars are average value for the 25 and the 75% percentiles in the 43 years for the 0-2.0 m soil profile.

Cumulative N mineralisation from 15 August to 1 May was on average (over 43 years) 56, 77 and 88 kg N ha^{-1} y^{-1} for bare soil, ryegrass and *Brassica* simulations. As mineralisation from catch crop

residues occurred in the upper soil layers and relatively late in the simulation period, there was a clear tendency in all three soil texture classes for catch crops to increase inorganic N content in the uppermost soil layers.

Mineral N in soil after catch crops

As mentioned, the catch crops reduced the mineral N content of the soil layers below 0.25 m in the autumn, and due to its deeper root growth, *Brassica* reduced the N content more efficiently than ryegrass (Figure 4a). This difference in subsoil mineral N content was still clearly visible in the 0.75-2.0 m layer in the sandy loam and loamy sand soils in May (Figure 4b), but not in the sandy soil, where practically all subsoil N was lost through leaching between December and May.

Catch crops also affected the content of mineral N in spring in the surface layer by mineralisation of crop residues. Simulations with *Brassica* showed the highest topsoil mineral N content in the spring (Figure 4b), reflecting its deep rooting and high N uptake from the whole soil profile in the autumn, but also the fact that it was parameterised to have a lower C/N ratio in its dry matter, and thereby a higher relative N mineralisation from its residues.

In the sandy soil, the only difference between ryegrass (limited rooting depth) and *Brassica* (deep rooting) was a higher mineralisation from *Brassica*, increasing topsoil mineral N content as mentioned above. While catch crops increased the total content of mineral N in the sandy soil, they decreased total N content in the heavier soils, as the reduction in N content below 0.75 m was greater than the increase in N content in the upper 0.25 m layer. In all combinations, catch crops changed the depth distribution of mineral N in the soil, leaving a higher fraction of soil N in the topsoil than bare soil (Figure 4b). This effect was always stronger with *Brassica* than with ryegrass because of the more efficient subsoil N depletion and the higher N mineralisation in the topsoil.

Leaching of nitrate out of the soil profile at 2.0 m depended on the soil texture class. Catch crop had a strong effect on the sandy soil in 41 of the 43 years simulated (Figure 5). On loamy sand and especially sandy loam, where nitrate retention was higher and leaching losses lower in simulations without crops, the effect of the catch crops was smaller, 10-30 kg N ha^{-1} in 20% of the years simulated for loamy sandy and 60% of those simulated for sandy loam (Figure 5). The use of catch crops affected the amount and the distribution of plant-available N in the soil profile in May. In sandy soils with high precipitation, use of ryegrass and *Brassica* had a positive N effect (N_{eff}, mineral N content after a catch crop compared with mineral N content after bare soil) of on average 15 and 29 kg N ha^{-1} (Figure 4b) respectively. The between-year variation in N_{eff} of both catch crops was relatively low for the sandy soil in the high precipitation regime, with only a few of 43 years simulated showing negative N_{eff} values (Figure 6). However, average N_{eff} on sandy soil was lower in the medium precipitation regime and close to zero in low precipitation regimes, where more N was retained in the bare soil simulations (data not shown). On loamy sand and sandy loam, negative N_{eff} values were found when the entire 0-2 m profile was taken into account. For ryegrass, average values ranged from -18 to -33 kg N ha^{-1} and for *Brassica* from -25 to -49 kg N ha^{-1} in the simulations shown in Figure 4b. However, with the high precipitation regime, catch crops showed N_{eff} values of around zero (data not shown). The between-year variation in N_{eff} for both catch crops was relatively higher (Figure 6, centre and bottom graphs) in the medium and low precipitation regimes. Thus N_{eff} depended strongly on N retention in the bare soil simulations; where this was low, positive N_{eff} values were found, but where bare soil retention was higher, N_{eff} became lower and often negative.

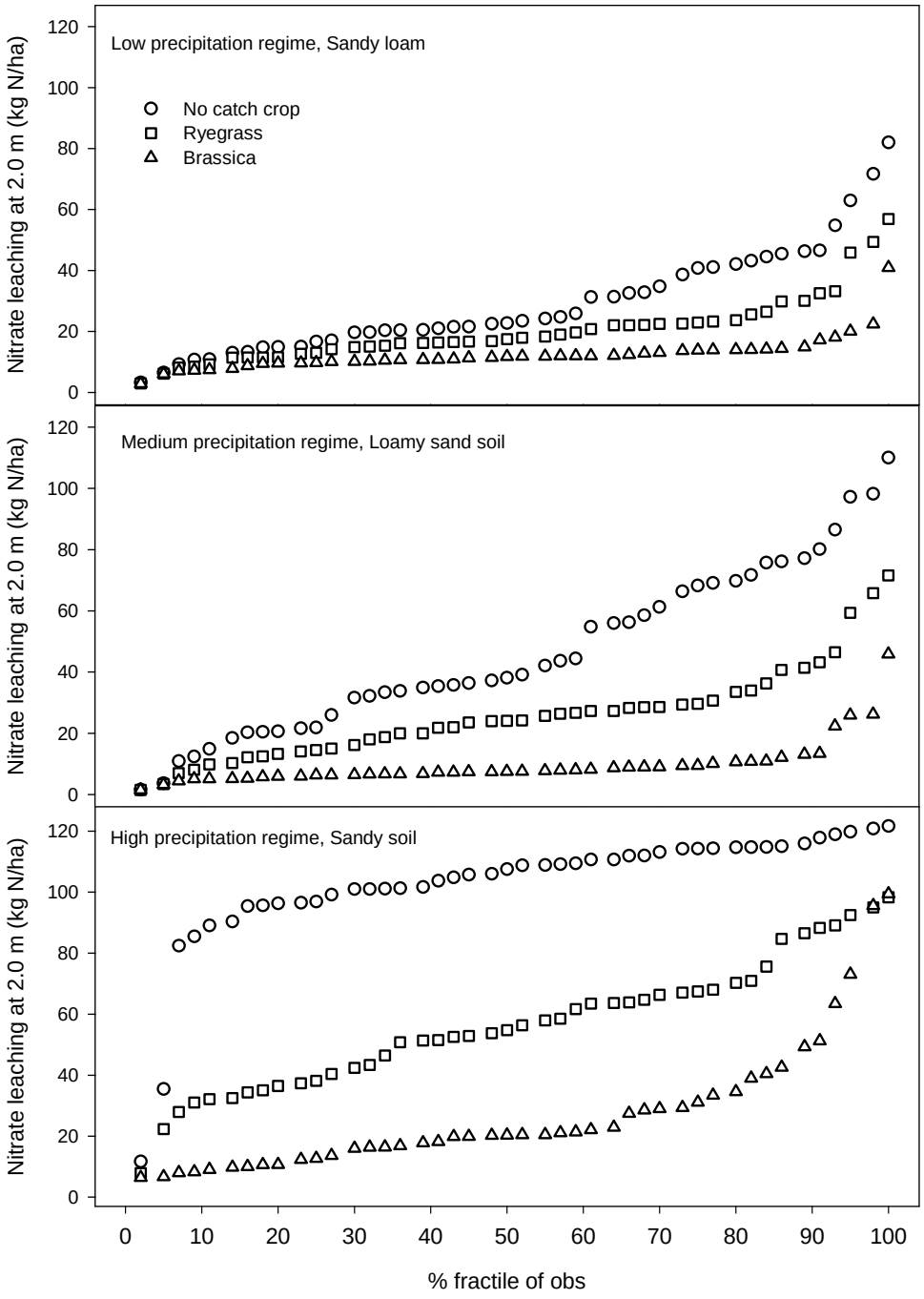

Figure 5. Fractile distribution of the between-year variation in fraction of nitrate leaching at 2.0 m on 1 May in the same simulations as in Figure 4. Simulations with climate data from 43 years and either low precipitation and sandy soil, medium precipitation and loamy sand soil or high precipitation and sandy loam. Key to symbols within diagram.

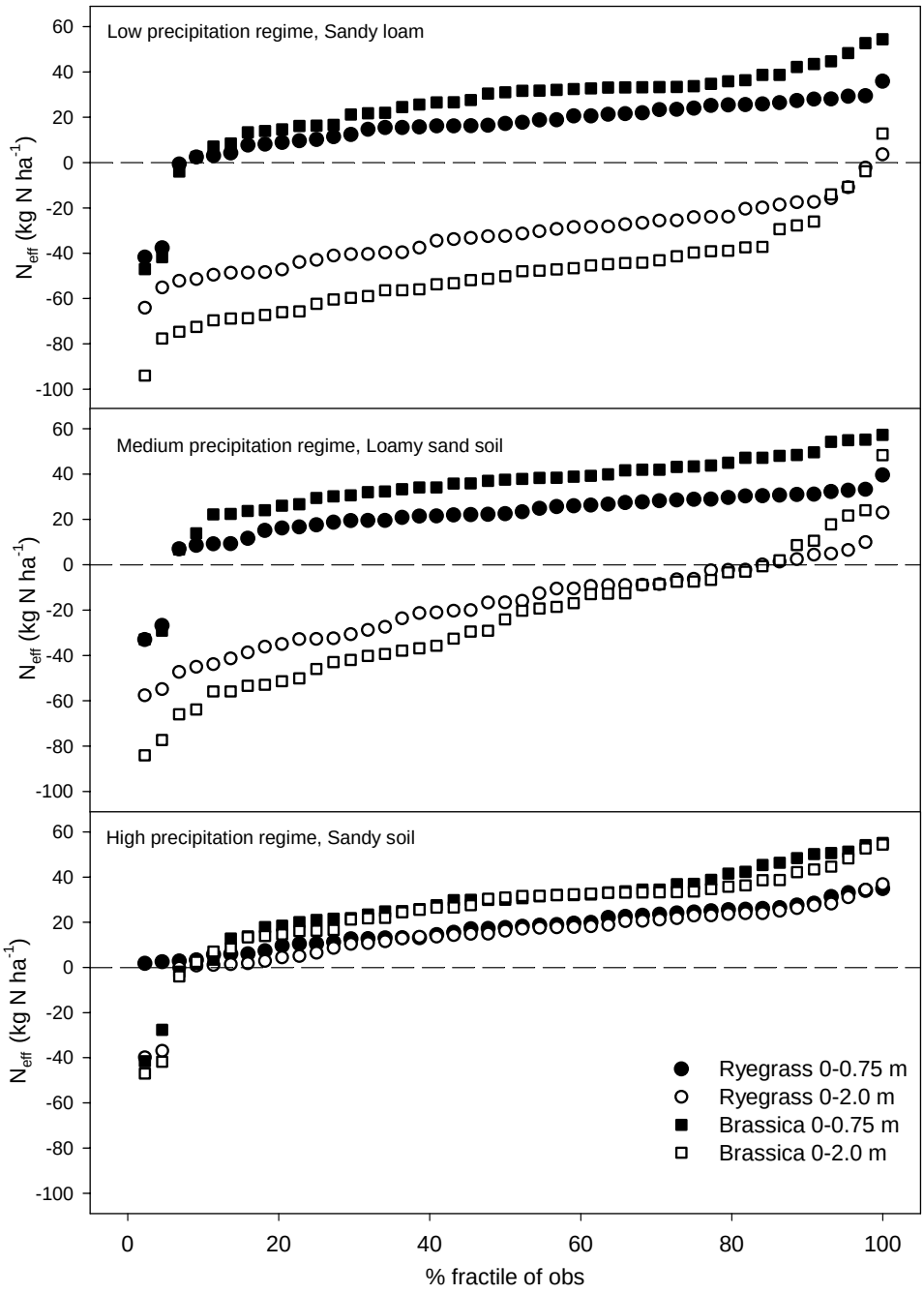

Figure 6. Fractile distribution of the between-year variation in N_{eff} (for definition, see text) for catch crop use in 0-0.75 layer and 0-2.0 m soil profile on 1 May. Simulations with climate data from 43 years and either low precipitation and sandy soil, medium precipitation and loamy sand soil or high precipitation and sandy loam. Key to symbols within diagram.

The N_{eff} values for both catch crops were positive in all three soil texture classes in the topsoil layer and the *Brassica* catch crop increased the N content in sandy loam soil by 34 kg N ha^{-1}, while

ryegrass increased it by 21 kg N ha^{-1} (Figure 4b). In combinations with high precipitation and sandy soil, increased N content was also to some extent found in the 0.25-0.75 m soil layer.

In the deepest soil layer, available N was low and unaffected by catch crops on the sandy soil. However, on loamy sand and sandy loam a strongly negative N_{eff} of catch crops was found in the 0.75-2.0 m soil layer, as the N content was only 9 kg N ha^{-1} after *Brassica*, 35 kg N ha^{-1} after ryegrass and as high as 83 kg N ha^{-1} in bare soil.

Thus the simulations show that while catch crops always increased N availability for following shallow-rooted main crops, the N_{eff} for following deep-rooted main crops was lower. On heavier soils, where N retention was higher in bare soil simulations, N_{eff} was generally negative.

Discussion

Retention of nitrate in bare soil

Soil texture and precipitation regimes interact in their influence on the fraction of nitrate retained in the spring, as shown with the present sets of simulations. The sandy soil had very low retention in all precipitation regimes, whereas loamy sand and sandy loam showed higher retention with decreasing precipitation. This was also found in field trials in Denmark with similar soil texture and precipitation regimes (Askegaard *et al*., 2005). The present simulation study can also be evaluated against a more detailed field study of water flow, nitrate retention and nitrate leaching (Djurhuus *et al*., 1999). In that experiment, nitrate concentrations were measured at 0.25 and 0.8 m depth in sandy soil and loamy sand soil during late autumn and winter. In the sandy soil a peak nitrate concentration at 0.8 m depth appeared around 1 November, but by January the nitrate had already leached away from this layer again. On the sandy loam the nitrate peak at 0.8 m depth was observed later, in January. During the rest of the winter and early spring the nitrate concentration fell only slowly and in April a substantial amount of nitrate was still retained at 0.8 m depth (Djurhuus *et al*., 1999) which is comparable with the simulations.

Although it can be expected that soil nitrate retention without the use of catch crops would be affected by soil texture and precipitation regimes, the large magnitude of between-year variation in soil nitrate retention has not been commonly recognised. For a similar simulation study over 10 years under English and Welsh weather conditions, Burns (1984) showed relative retention within the top 1.0 m of the soil in different regions ranging from 0.15 to 0.48 in sandy soil and 0.24 to 0.64 in loamy sand. That study only examined the winter season, whereas the present simulations extended from 15 Aug to 1 May. However Burns (1984) showed the same high variations in precipitation and retained fraction of nitrate as under Danish conditions. Within most of the soil type and climate combinations examined here, the retention varied from close to nil up to almost

100%. This highlights the fact that interpretations based on average or median values of weather conditions across years may not serve as a good base for management decisions.

With information about soil texture and actual climatic regime for the location, the curve in Figure 2 that best describes a specific year could be determined. Sandy soil, with low water-holding capacity, had low nitrate retention even in relatively dry years. However, the simulations showed a higher retention in the few driest years of the simulations, where much retained nitrate was found below 1.0 m.

Generally, we found most of the N retention to be in the deeper soil layers, and therefore simulating to a depth of 2 m, rather than the 1 m or less typically used for mineral N measurements in experimental field studies of nitrate leaching or for N fertilisation recommendation, can have a strong influence on the conclusions drawn, at least when the crop rotation includes deep-rooted crops that can access this deep mineral N.

The model simulations showed that retained N was almost exclusively found in deeper soil layers. Field studies show the same effect, as high nitrogen addition as fertiliser or plant residues leads to increased subsoil mineral N content in the following spring, whereas topsoil mineral N level is not affected (Sainju *et al*., 1999; Thorup-Kristensen, 2006b). Even though nitrate is sometimes retained in deep layers in sandy soil, this may be less valuable than nitrate retained in deep layers in soils with higher clay content, as sandy soil tends to limit root growth by mechanical impedance (Greacen, 1986; Henderson *et al*., 1988). Higher clay content allows deeper rooting, due to lower mechanical impedance and a more structured soil matrix, and the roots of some crop species are able to take up N from soil layers down to 2.0 m (Gregory *et al*., 1978; Barraclough, 1989), some even deeper.

Mineral N in soil after catch crops

In the late autumn soil nitrate content under catch crops was low in the 0-0.75 m soil layer, where both catch crops had roots. *Brassica* also took up N from the 0.75-2.0 m layer, while ryegrass did not have roots in this layer (the maximum root depth in the simulation was set to 0.7 m for ryegrass and 2 m for *Brassica*). In years with a high cumulative temperature during autumn the roots reached these maximum depths, in agreement with field experiments (Barraclough, 1989; Smit and Groenwold, 2005; Thorup-Kristensen, 2001; Thorup-Kristensen, 2006b). Field studies show a rapid root extension, rooting depth development and high subsoil root intensity for *Brassica* species (Thorup-Kristensen, 2006b), and *Brassica* therefore has the ability to reduce the nitrate concentration directly in soil layers below 1.0 m.

In spring, the level of mineral N in the 0-0.25 m soil layer was higher after *Brassica* than ryegrass in all three soil classes. In the present simulations, catch crops were incorporated on 1 Dec to simulate the effect of a long period of mineralisation. *Brassica* had a higher N uptake due to deeper rooting, and it was parameterised to have a lower C/N ratio than ryegrass. These differences agree with experimental results and led to higher mineralisation rates, as also shown in several laboratory and field studies (Jensen, 1992; Thorup-Kristensen, 1994; Jensen *et al*., 2005). Later incorporation of the catch crops, e.g. in early spring, would produce different mineralisation patterns compared with the date used here (1 Dec). Winter-hardy catch crops, such as ryegrass, often stay green and continue growth in warm winters, taking up N during the winter and spring period, resulting in low mineral N content. Furthermore, a period of N immobilisation can be expected immediately after incorporation due to a relatively high C/N ratio (Thorup-Kristensen *et al*., 2003). Non winter-hardy crops such as white mustard or oil radish die down in the first frost events of winter and start N mineralisation shortly afterwards. In addition, non winter-hardy crops such as *Brassica* often drop their leaves in warm winters and therefore produce continuous N mineralisation from the decaying

leaves during winter, resulting in a higher level of mineral N in soil at incorporation compared with ryegrass (Thorup-Kristensen *et al*., 2003).

The simulations showed less mineralisation from catch crops than found in field studies (Thorup-Kristensen, 2006a; Thorup-Kristensen, 2006b; Vos and van der Putten, 2001). The mineralisation may have been underestimated during winter, as the model simulates very little turnover at temperatures below 5 °C, while field and detailed laboratory studies indicate that N mineralisation may proceed at lower temperatures (Breland, 1994; Thorup-Kristensen, 1994; Andersen and Jensen, 2001; Magid *et al*., 2001).

In the deep subsoil (0.75-2.0 m), the average amount of mineral N was higher after ryegrass than after *Brassica* on the loamy sand and sandy loam soils. A study by Thorup-Kristensen (2006b) showed this effect in one year of two. In the first year they found a very low mineral N content under both ryegrass and a *Brassica* catch crop in the autumn, and no difference in deep soil mineral N in spring after ryegrass and *Brassica*. In the second year ryegrass did not deplete the soil inorganic N pool below 0.5 m very well, while the *Brassica* crop did. In the spring of that year, higher levels of inorganic N content were seen in the subsoil after ryegrass, as found in the present simulation studies. Thus simulations and experiments show that deep soil nitrate left under more shallow-rooted catch crops may be retained until the following spring.

Retention of mineral N in the subsoil after ryegrass was scarcely found on the sandy soil (only in 2 out of 43 years) in any of the precipitation regimes. Retention was low here, as mentioned for the bare soil simulations, and therefore no effect of using medium- or deep-rooted catch crops was seen in the subsoil. The availability of nitrate in spring in the subsoil after a medium-rooted catch crop will thus increase with decreasing precipitation and increasing clay content.

Interactions of bare soil and catch crops on nitrate retention in spring

The nitrogen effect (N_{eff}) of catch crops, measured as soil inorganic N content in the following spring, is the combined effect of autumn soil N depletion by catch crop N uptake and N mineralisation from catch crop residues after incorporation. The present simulations show that average N_{eff} for the 0-2.0 m soil profile was positive in sandy soil and negative in loamy sand and sandy loam soils in most years (Figure 6). This result was found even though spring soil N content after catch crops tended to be higher on loamy sand and sandy loam soils than on the sandy soil. The main difference was found in the amount of N retained in the bare soil simulations. Here very little was retained in the sandy soil, and only in very dry years did N_{eff} become negative (Figures 3 and 7). The higher N retention found on the heavier soils resulted in mostly negative N_{eff} values, and only in the wettest years was a positive N_{eff} simulated (Figure 6). However, when only the top 0-0.75 m layer was considered, the situation was reversed; N_{eff} values were generally positive, except in the driest years.

When N retention in bare soil is low, as is the case on sandy soils in a wet climate, N_{eff} is determined mainly by mineralisation of catch crop residues in spring and is normally positive (Thorup-Kristensen and Nielsen, 1998; Thorup-Kristensen *et al.*, 2003). When N retention in bare soil is high, whether this is caused by soils with high water retention or by low precipitation on more sandy soils, N_{eff} is often negative, as the N content in the soil after catch crops is then compared with high N contents where no catch crop was grown. Field studies have also shown that catch crops may reduce nitrogen availability for following crops, even when net N mineralisation from their residues is found. This effect has been termed pre-emptive competition (Thorup-Kristensen, 1993), and occurs because catch crops take up available soil N that could instead have been retained and used directly by the next crop (Thorup-Kristensen, 1993). Such pre-emptive

competition can also be seen in the results of a range of short-term field experiments (Jensen, 1992; Torstensson and Aronsson, 2000).

In a two-year field experiment, Willumsen and Thorup-Kristensen (2001) showed two extremes in spring mineral N content without catch crops, because of one very wet and one very dry winter season. In this experiment N_{eff} was negative after the dry winter season and positive after the wet season. In data from 13 years with catch crop experiments at a sandy loam soil site, the spring mineral N content without catch crops was high after dry winter seasons and low after wet winter seasons, whereas spring soil mineral N content after catch crops was relatively unaffected by winter season precipitation (Thorup-Kristensen *et al*., 2003). This led to negative catch crop N_{eff} in years receiving less than 400 mm precipitation during autumn and winter, and positive N_{eff} when precipitation exceeded 500 mm. In a seven-year field experiment using clover grass as a catch crop, a positive effect on spring barley yield was observed in six years in sandy soil but only in two years in loamy sand and sandy loam (Olesen *et al*., 2007).

The results show that N_{eff} depends strongly on the soil layer considered. When only the top 0.25 m was considered, a positive N_{eff} was observed in all the three climatic regimes and the three soil texture classes examined here. N_{eff} was also mostly positive when the 0-0.75 m soil layer was considered, but N_{eff} was lower when the whole 0 to 2 m soil profile was considered, and as just discussed, it was then mostly negative on loamy sand and sandy loam soils (Figure 7). Comparisons with experimental field data from Denmark (Thorup-Kristensen *et al*., 2003) show a high degree of agreement with these simulated patterns, as illustrated in Figure 7. In both the measured and simulated data, a strong positive N_{eff} can be seen when considering only the top 0.25 m of the soil, but this becomes negative when the whole soil profile to 1.5 or 2 m depth is taken into account (Figure 7).

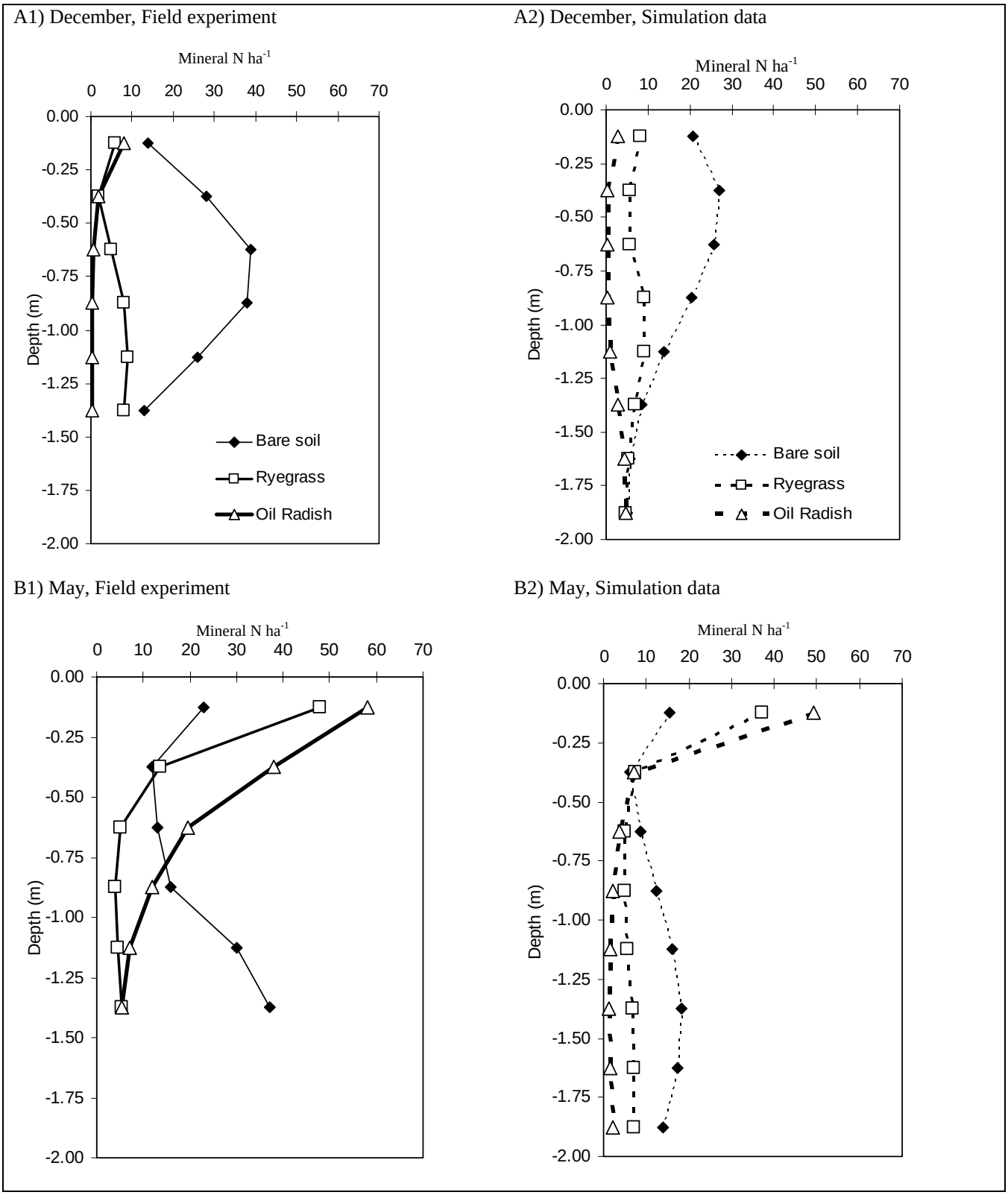

Figure 7. Measured and simulated soil mineral N in December and May. For A1 and B1 field experiment (average of 2 years) with no catch crop, ryegrass and *Brassica*, taken from Thorup-Kristensen (2001). For A2 and B2 simulation for no catch crops and use of ryegrass and *Brassica* as catch crops in a sandy loam soil placed in medium precipitation regime.

Without catch crops, mineral N content in the upper soil layers is often low, as shown by Thorup-Kristensen *et al*. (2003), who found that spring mineral N content in the 0-0.5 m layer exceeded 50 kg N ha^{-1} in only one very dry year out of 13 years, and therefore a positive N_{eff} of catch crops was observed in this soil layer, whereas higher retention in the subsoil led to lower N_{eff} values when a deeper soil profile was considered (Thorup-Kristensen, 1994; Thorup-Kristensen and Nielsen, 1998). This relationship between soil depth considered and the N_{eff} values obtained suggest that crops with limited rooting depth can preferably be grown after a catch crop in all the precipitation and soil regimes tested in the simulations, whereas deep-rooted crops might experience negative N_{eff} after the same catch crops. Such effects have also been seen in field experiments, where catch crop use resulted in positive N_{eff} for following onions, beetroot and leeks, but negative N_{eff} for a following deep-rooted white cabbage crop (Willumsen and Thorup-Kristensen, 2001Thorup-Kristensen, 2006a; Thorup-Kristensen, 2006b).

The present results show that the model can be used to predict the combinations of catch crops and following crops that give the optimal crop N supply in a certain climate and soil type, and to predict when there is a risk of negative N_{eff} from growing a particular catch crop. These predictions can be used by farmers to plan their rotations and adjust their fertilisation plans, provided that they are embedded in a decision-support system.

Conclusions

The simulations showed low nitrate retention in topsoil layers in all three climatic regimes and soil texture classes examined. Nitrate retention increased greatly with depth in all soil types under low precipitation, while with higher precipitation this increase was mainly seen on soils with higher clay content. These patterns correspond well with those reported in field trials.

The simulated deep-rooted *Brassica* catch crop clearly depleted autumn soil mineral N much more efficiently than the simulated shallow-rooted ryegrass, in particular in the subsoil (0.75-2.0 m). However, the difference in effect of the two catch crops on nitrate availability in the following spring was more in terms of distribution with depth than in total amount, *Brassica* producing a higher proportion of mineral N in the topsoil (0-0.25 m) than ryegrass on all soils and climatic regimes.

The simulated nitrogen effect (N_{eff}) of the catch crops was clearly influenced by autumn soil N depletion by the catch crop and N mineralisation from the catch crop, but especially by indigenous nitrate retention in the soil without catch crops. Very little mineral N was retained over winter in sandy soil without a catch crop, and hence generally positive N_{eff} values were found, whereas the higher N retention found on the heavier soils resulted in mostly negative N_{eff} values.

However, when only the top 0-0.75 m layer was considered, N_{eff} values were generally positive, except in the driest years, and therefore the rooting depth of the following crop was shown to greatly influence the expected N_{eff}.

Finally, the inclusion of 43 years of climatic data clearly illustrated that between-year variation in precipitation may greatly influence the conclusions about N_{eff}; in particular for more deep-rooted crops where in an intermediate climatic regime N_{eff} may be anything from strongly negative to positive. However, the current results can be used to calculate the probability of positive or negative

N_{eff} from growing a particular catch crop – main crop sequence in a given climate and soil type. If such predictions are embedded in a farmer's decision-support system, they can be valuable for planning rotations and adjusting fertilisation applications.

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References

Abrahamsen, P. & Hansen, S. 2000. Daisy: an open soil-crop-atmosphere system model. *Environmental Modelling and Software* **15**, 313-330.

Allerup, P., Madsen, H. & Vejen, F. 1998. Standardværdier (1961-90) af nedbørkorrektioner (In Danish). *Danish Meteorological Institute*, Copenhagen.

Andersen, M.K. & Jensen, L.S. 2001. Low soil temperature effects on short-term gross N mineralisation-immobilisation turnover after incorporation of green manure. *Soil Biological Biochemistry*. **33**, 511-521.

Anonymous, 2000. Directive 2000/60/EC of the European parliament and of the council of 23 October 2000 establishing a framework for the Community action in the field of water policy. *Official Journal of the European Communities* **L 327**, 1-72.

Askegaard, M., Olesen, J.E. & Kristensen, K. 2005. Nitrate leaching from organic arable crop rotations: effects of location, manure and catch crop. *Soil Use and Management* **21**, 181-188.

Barraclough, P.B. 1989. Root growth, macro-nutrient uptake dynamics and soil fertility requirements of a high yielding winter oilseed rape crop. *Plant and Soil* **119**, 59-70.

Breland, T.A. 1994. Enhanced mineralization and denitrification as a result of heterogeneous distribution of clover residues in soil. *Plant and Soil* **166**, 1-12.

Burns, I.G. 1984. Estimation of annual variations in leaching of residual nitrate under deep-rooted crops during winter. In: *The nitrogen requirements of cereals*, MAFF/ADAS Reference book 385. London: Her Majesty's Stationary Office 95-101.

de Willigen, P. 1991. Nitrogen turnover in the soil-crop-systems: Comparison of fourteen simulation models. *Fertilizer Research* **27**, 141-149.

Diekkrüger, B., Söndgerath, D., Kersebaum, K.C. & McVoy, C.W. 1995. Validity of agroecosystem models. A comparison of results of different models applied to the same data set. *Ecological Modelling* **81**, 3-29.

Djurhuus, J., Hansen, S., Schelde, K. & Jacobsen, O.H. 1999. Modelling mean nitrate leaching from spatially variable fields using effective hydraulic parameters. *Geoderma* **87**, 261-279.

Elers, B. & Hartmann, H.D. 1987. Biologische Konservierung von Nitrat. *Gemüse* **4**, 210-214.

Ellerman, T., Hertel, O., Kemp, K. & Monies, C. 2002. Atmosfærisk deposition, 2001 (In Danish). *NOVA* 2003.

Frich, P., Rosenørn, S., Madsen, H. & Jensen, J.J. 1997. Observed Precipitation in Denmark 1961-90. pp. 1-40. *Danish Meteorological Institute*, Ministry of Transport, Copenhagen.

Greacen, E.L. 1986. Root response to soil mechanical properties. *Soil Science* **5**, 20-47.

Gregory, P., McGowan, M., Biscoe, P.V. & Hunter, B. 1978. Water relations of winter wheat. 1. Growth of the root system. *Journal of Agricultural Sciences 91*, 21-102.

Hansen, S., Jensen, H.E., Nielsen, N.E. & Svendsen, H. 1991. Simulation of nitrogen dynamics and biomass production in winter wheat using the Danish simulation model daisy. *Fertilizer Research* **27**, 245-259.

Henderson, C., Levett, A. & Lisle, D. 1988. The effects of soil water content and bulk density on the compactibility and soil penetration resistance of some Western Australian sandy soils. Australian *Journal of Soil Research* **26**, 391-400.

Jensen, E.S. 1992. The release and fate of nitrogen from catch-crop materials decomposing under field conditions. *Journal of Soil Science* **43**, 335-345.

Jensen, L.S., Salo, T., Palmason, F., Breland, T.A., Henriksen, T.M., Stenberg, B., Pedersen, A., Lundström, C. & Esala, M. 2005. Influence of biochemical quality on C and N mineralisation from a broad variety of plant materials in soil. *Plant and Soil* **273**, 307-326.

Kristensen, H.L. & Thorup-Kristensen, K. 2004. Root Growth and Nitrate Uptake of Three Different Catch Crops in Deep Soil Layers. *Soil Science Society of America Journal* **68**, 529-537.

Magid, J., Henriksen, O., Thorup-Kristensen, K. & Mueller, T. 2001. Disproportionately high N-mineralisation rates from green manures at low temperatures - implications for modeling and management in cool temperate agro-ecosystems. *Plant and Soil* **228**, 73-82.

Mueller, T., Thorup-Kristensen, K., Magid, J., Jensen, L.S. & Hansen, S. 2006. Catch crops affect nitrogen dynamics in organic farming systems without livestock husbandry - Simulations with the DAISY model. *Ecological Modelling* **191**, 538-544.

Olesen, J.E., Hansen, E.M., Askegaard, M. & Rasmussen, I.A. 2007. The value of catch crops and organic manures for spring barley in organic arable farming. *Field Crops Research* **100**, 168-178.

Sainju, U.M., Singh, B.P., Rahman, S. & Reddy, V.R. 1999. Soil nitrate-nitrogen under tomato following tillage, cover cropping, and nitrogen fertilization. *Journal of Environmental Quality* **28**, 1837-1844.

Smit, A.L. & Groenwold, J. 2005. Root characteristics of selected field crops: Data from the Wageningen Rhizolab (1990–2002). *Plant and Soil* **272**, 365-384.

Thorup-Kristensen, K. 1993. The Effect of Nitrogen Catch Crops on the Nitrogen Nutrition of a Succeeding Crop I. Effects through Mineralization and Pre-emptive Competition. *Acta Agriculturae Scandinavica Section B - Soil and Plant Science* **43**, 74-81.

Thorup-Kristensen, K. 1994. The effect of nitrogen catch crop species on the nitrogen nutrition of succeeding crops. *Fertilizer Research* **37**, 227-234.

Thorup-Kristensen, K. 2006a. Root growth and nitrogen uptake of carrot, early cabbage, onion and lettuce following a range of green manures. *Soil Use and Management* **22**, 29-39.

Thorup-Kristensen, K., Magid, J. & Jensen, L.S. 2003. Catch crops and green manures as biological tools in nitrogen management in temperate zones. *In Advances in Agronomy*. Ed. Sparks. pp. 227-302. Academic Press.

Thorup-Kristensen, K. 2001. Are differences in root growth of nitrogen catch crops important for their ability to reduce soil nitrate-N content, and how can this be measured? *Plant and Soil* **230**, 185-195.

Thorup-Kristensen, K. 2006b. Effect of deep and shallow root systems on the dynamics of soil inorganic N during 3-year crop rotations. *Plant and Soil* **288**, 233-248.

Thorup-Kristensen, K. & Nielsen, N.E. 1998. Modelling and measuring the effect of nitrogen catch crops on the nitrogen supply for succeeding crops. *Plant and Soil* **203**, 79-89.

Torstensson, G. & Aronsson, H. 2000. Nitrogen leaching and crop availability in manured catch crop systems in Sweden. *Nutrient Cycling in Agroecosystems* **56**, 139-152.

Vos, J. & van der Putten, P.E.L. 1997. Field observations on nitrogen catch crops. I. Potential and actual growth and nitrogen accumulation in relation to sowing date and crop species. *Plant and Soil* **195**, 299-309.

Vos, J. & van der Putten, P.E.L. 2001. Field observations on nitrogen catch crops. III. Transfer of nitrogen to the succeeding main crop. *Plant and Soil* **236**, 263-273.

Vos, J., van der Putten, P.E.L., Hussein, H.M., van Dam, A.M. & Leffelaar, P.A. 1998. Field observations on nitrogen catch crops. *Plant and Soil* **201**, 149-155.

Willumsen, J. & Thorup-Kristensen, K. 2001. Effects of green manure crops on soil mineral nitrogen available for organic production of onion and white cabbage in two contrasting years. *Biological Agriculture & Horticulture* **18**, 365-384.

Paper III:

Anders Pedersen, Kefeng Zhang, Kristian Thorup-Kristensen and Lars Stoumann Jensen. Simulating root density dynamics and nitrogen uptake in the soil profile – A simple approach. In preparation.

Simulating root density dynamics and nitrogen uptake in the soil profile – A simple approach

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Abstract

We present a 2-D model for simulation of root density and nitrogen (N) uptake for crops grown in agricultural systems, based on a modification of Gerwitz and Page's (1974) original root density equation. A root system form parameter was introduced to describe the distribution of root biomass vertically and horizontally in the soil profile. The form parameter can vary from 0 where root density is evenly distributed in the soil profile, to 8 where practically all roots are found near the surface. The root model has other components describing root features, such as specific root length and N uptake kinetics.

The rooting depth penetration rate and depth distribution of root density were found to be the most important parameters controlling crop N uptake from deeper soil layers. The validity of the root distribution model was tested with field data for white cabbage, red beet, and leek. The root density for white cabbage was high in the whole soil profile, with the simulated distribution decreasing in deeper soil layers. The model was able to simulate N depletion in different soil layers in a field study for crops with different rooting depths and depth distribution and different amounts and distribution of soil mineral N in spring. This shows the sensitivity of the form parameter value and the ability of the selected parameter to reproduce N depletion in soil layers. This work provides a simple root model driven by degree days and simulated crop growth and with a requirement of few measured parameters.

Keywords: EU_rotateN, modelling nitrogen uptake, root distribution parameter, root modelling.

List of abbreviations, initial value if needed, units and explanation

Name	Default value	Unit	Explanation
Model parameters			
a_z	[0,1..8]	-	Form parameter, vertically
a_x	[0,1..8]	-	Form parameter, horizontally
$c_{\min}$	5.0	[kg N 0.05 m^{-2} ha^{-1}]	Minimum nitrate or ammonium concentration in soil layer
Kf	1.45	-	Plant N uptake coefficient
kN	0.07	-	Plant N uptake coefficient
k_{rz}	-	[m day^{-1} $°C^{-1}$]	Vertical root penetration rate parameter
k_{rx}	-	[m day^{-1} $°C^{-1}$]	Horizontal root penetration rate parameter
q	1.3	-	Absolute rooting depth relative to simulated rooting depth
R_x	-	[m]	Root system width
R_z	-	[m]	Vertical root depth
$R_{z\text{-}max}$	-	[m]	Maximum rooting depth
$R_{z\text{-}min}$	0.10	[m]	Starting depth of the seed or plant
S_r	300000	[m g^{-1}]	Specific root density
T_{max}	30	[°C]	Maximum temperature for root growth
T_{min}	0	[°C]	Minimum temperature for root growth
DD	-	-	Day-degrees
DD_{lag}	-	[DD]	Lag phase for initiating root growth
T	-	[°C]	Temperature
T_{lag}	-	[DD]	Lag phase for initiating root growth
L_0	-	[m m^{-3}]	Root density at surface
L_r	-	[m m^{-2}]	Total root length
L_z	-	[m m^{-3}]	Root density at soil depth z
N_{demand}	-	[kg N ha^{-1} d^{-1}]	Nitrogen demand calculated
$N_{pot}(i,j)$	-	[kg N ha^{-1}]	Potential nitrate or ammonium uptake each soil unit (i,j)
N_{up}	-	[kg N ha^{-1}]	Actual nitrate and ammonium plant uptake
W_r	-	[g m^{-2}]	Root biomass
z	-	[m]	Soil depth
c	-	[kg N ha^{-1}]	Nitrate or ammonium concentration

Introduction

Plant and soil models are commonly used to predict crop yield and the environmental impact of crop production. Such models often combine complex modelling of water movement, soil organic matter turnover and aboveground plant growth. Simulation of root growth is an important part, because roots are the link between mineral N in soil and plant N in the models. While the simulation of aboveground plant growth has become increasingly advanced over the years, root modelling has remained fairly simple due to the lack of field data to calibrate more sophisticated root models at field scale. Some root models including detailed modelling of individual roots have been developed (Dunbabin et al., 2002; Kohl et al., 2007; Pages et al., 2004). However, such models are mainly used for scientific work and are generally not suitable for simulation of real crop rotations because of a lack of input data and because the models are often only developed for one or a few plant species.

Recent field studies have shown that the development of crop rooting depth can be described by a lag phase starting at sowing or transplanting, after which root depth increases linearly with temperature sum (Kage et al., 2000; Smit and Zuin, 1996; Thorup-Kristensen and Van den Boogaard, 1998).

Rooting depth and root architecture differ significantly between crop species (Kutschera, 1960; Weaver, 1926). For monocot species, root penetration rates in the range of about 0.02 cm day-degree^{-1} have been observed for onion (Thorup-Kristensen, 2006a) and 0.08 to 0.12 cm day-degree^{-1} for cereals and grasses (Thorup-Kristensen, 2001a). For dicot species, penetration rates are about 0.07 cm day-degree^{-1} for carrot and between 0.12 to 0.25 cm day-degree^{-1} or even higher for white cabbage and fodder radish (Smit and Groenwold, 2005; Thorup-Kristensen, 2001a). Final rooting depth is related to penetration rate and length of growing season. Thus onions develop only a very

shallow root system down to approximately 0.2 to 0.3 m (Burns, 1980; Thorup-Kristensen, 2001a), ryegrass roots grow to approximately 1 m (Kristensen and Thorup-Kristensen, 2004) and white cabbage, red beet and fodder radish can grow to 2 m or more (Kristensen and Thorup-Kristensen, 2004; Thorup-Kristensen, 2006b), provided that root growth is not impeded by soil compaction or coarse soil texture.

Monocots and some dicot species have their highest root length densities near the surface, as observed in winter wheat (Asseng et al., 1997; Xue et al., 2003; Zuo et al., 2006), grasses (Smit and Groenwold, 2005; Thorup-Kristensen, 2001b) and cauliflower and spinach (Kage et al., 2000; Smit and Groenwold, 2005). Many dicot species have a more uniform distribution of root length density in the soil profile, often with higher root densities in deeper soil layers than monocot species, as found e.g. for oilseed rape (Barraclough, 1989) and fodder radish (Kristensen and Thorup-Kristensen, 2004; Smit and Groenwold, 2005). For crops grown as row crops, e.g. maize and many vegetable species, a significant difference in root density below and between rows has been shown for maize (Liedgens and Richner, 2001b), onion and carrot (Thorup-Kristensen, 2006a; Thorup-Kristensen and van den Boogaard, 1999), whereas lettuce and white cabbage typically show the same root density below and between rows already during their early growth (Thorup-Kristensen, 2006a).

The development and proliferation of the roots in soil are affected by intrinsic and extrinsic parameters such as the supply of photosynthates from the shoot, the nutrient status of the plant, soil type and compaction, water potential at the root surface and availability and distribution of nutrients (Bloom et al., 2003; Forde and Lorenzo, 2001). Root penetration rate in root models is often described as being affected by air or soil temperature and a plant-specific growth rate coefficient. The daily growth rate is associated with water stress, soil compaction, clay or sand content and

aeration (Penning de Vries et al., 1989; van Keulen and Seligman, 1987). The root model presented here is prepared for use of the above extrinsic factors and tested using parameter values based on field studies, but without any further reducing factors for water and clay content or soil compaction. Variation in bulk density at field scale at different soil depths is high and is likely to be important, but it is quite unrealistic to measure this for initiations of the model for field scale simulations.

A number of one-dimensional (1-D) models have been developed for modelling the soil-plant system to enable prediction of plant production, water and nitrogen dynamics in agricultural systems. In 1-D models, the soil column is divided into layers from the surface to a defined depth. Each layer can be assigned standard or specific parameters such as nutrient concentration, water content, temperature, bulk density, or soil strength. As 1-D models only distribute roots to a given soil depth, this limits the capability of the model to take into consideration the uneven root distribution of row crops. Two-dimensional (2-D) and three-dimensional (3-D) root models, on the other hand, are able to simulate spatial differences in nutrient uptake and root distribution of row crops, which leads to much more complex soil water and N dynamics.

Gerwitz and Page (1974) introduced a logarithmic function for root density calculations in 1-D systems. The function gives the percentage of roots for a given rooting depth, with the highest root density near the soil surface. The function has been modified and used in the Daisy model by Abrahamsen and Hansen (Abrahamsen and Hansen, 2000). Here root density is set to a very low default value at the bottom of the rooting zone, so variations in total root length have little effect on subsoil root length and all variation is confined to the surface soil layers.

In this work we present a model for root growth and proliferation of root length density in the soil profile, assess whether this model is able to simulate a range of crop root systems, their N uptake and their soil N depletion, and compare these against experimental field data. The purpose of this

root model is to model a variety of arable and vegetable crop species and reproduce results from field experiments for N depletion with a simple root modelling approach and a minimum of parameters and input requirements.

The objective of the present work was to test the ability of the newly developed root model to simulate root development and N depletion in the soil profile as known from the literature and to compare simulated soil N depletion against field observations for vegetable crops with different root patterns. The model was tested with respect to its: a) ability to simulate rooting depth and partitioning of root length density in the rooted zone, b) sensitivity of N uptake to parameter values determining root distribution and root growth and parameters determining root system N uptake efficiency, and c) root development and N uptake in row crops.

Materials and methods

Plant and soil modules

The root model operates as a module in an integrated soil-plant-atmosphere model. In brief, other modules in the model include an aboveground crop development and N demand module (Greenwood et al., 1996; Greenwood et al., 2001), a soil organic matter, soil microbial biomass and decomposition of added organic matter module from the Daisy model (Hansen et al., 1991) and a water balance module (Brisson et al., 2003).

The model runs on a daily basis. The information fed into the root module from other modules includes soil water content, ammonium and nitrate concentrations, root biomass increment and crop potential water and N demand, together with the climatic data, soil clay content and bulk density from the model run setup files. All processes are calculated in 0.05 m x 0.05 m grids within the soil domain of 2.0 m depth vertically and half the row width horizontally. Root density is calculated in

0.05 x 0.05 m girds, up to 1.0 m horizontally (controlled by row width) and to 2.0 m depth vertically, and when root depth or width enters the centre of a new grid, root density is calculated and N uptake occurs. For densely populated crops, the model operates in 1-D and only one soil column with 0.05 m width is considered.

Root module – 1-D model

Root penetration

Root growth calculation is based on cumulative day-degrees (DD) as shown in Equation 1.

Equation 1 $$DD = \sum T = \begin{cases} 0 & ;T_{\min} \geq T_{air} \\ T_{air} - T_{\min} & ;T_{\min} \leq T_{air} < T_{\max} \\ T_{\max} - T_{\min} & ;T_{air} \geq T_{\max} \end{cases}$$

A lag phase (DD_{lag}) in terms of DD is set to account for the period from seed germination or transplanting to root penetration. The root penetration depth (R_z) is calculated as follows.

Equation 2 $$R_z = \begin{cases} \mathrm{R}_{\text{z-min}} & ; \sum DD \leq DD_{lag} \\ \sum ((DD - DD_{lag})k_{rz}) + \mathrm{R}_{\text{z-min}} & ; \sum DD > DD_{lag} \\ R_{\text{z}-\max} & ; \sum DD - DD_{lag} k_{rz} + \mathrm{R}_{\text{z-min}} > R_{\text{z}-\max} \end{cases}$$

The calculation of root penetration in the horizontal direction is similar with Equation (2), and the calculation is restricted to the rooting depth. The initial root system starts with the root depth 0.1 m and begins to grow horizontally and vertically after the DD_{lag}. The model calculates the root

penetration depth until 2.0 m. $R_{z\text{-}max}$ is default 2.0 m and can be adjusted in the setup file for soil information.

Root density

The total root length (L_r) is calculated from root biomass (W_r) by assuming a specific root length density (S_r) (Equation 3). The equation for root density distribution is a modified form of the equation suggested by Gerwitz and Page (1974). In the present version, the root density declines by a logarithmic function down to the simulated rooting depth R_z, while below R_z it decreases linearly to zero at q=1.3 (Equation 4).

Equation 3 $$L_r = W_r S_r$$

Equation 4 $$L_z = \begin{cases} L_0 e^{(a_z z)} & ; z < R_z \\ L_0 e^{(a_z R_z)} \left(1 - \dfrac{z - R_z}{qR_z - R_z}\right) & ; qR_z > z > R_z \\ 0 & ; z > qR_z \end{cases}$$

Nitrogen uptake

Assuming a uniform distribution of roots in a soil grid, the potential nitrate and ammonium uptake in each grid is calculated by modifying the equation from Nielsen and Barber (1978) with root length as shown in Equation 5. The calculations for nitrate and ammonium uptake are similar, but they are calculated separately for each unit and accumulated for the whole soil profile. Ammonium only appears in the first 6 soil layers (0 - 0.30 m) in the model.

Equation 5 $$N_{pot}(i,j) = \frac{L_r \; kN \; (c - c_{\min})}{kf + c}$$

Actual N uptake is calculated from the potential N uptake in the rooted zone and the N demand comes as external information from the crop module. Equation 6 shows the calculation of actual N uptake.

Equation 6 $$N_{up} = N_{demand}\left(1 - e^{\left(-1\left(\frac{N_{pot}(NO_3^-) + N_{pot}(NH_4^+)}{N_{demand}}\right)\right)}\right)$$

2-D root system

In the 2-D model the soil domain is divided into a 0.05 m x 0.05 m grid. If a row crop has a row width greater than 0.1 m, the root module calculates root density in 2-D. The default root model assumes the same penetration rate in both directions, but different form parameters (a_z and a_x) are used for vertical and horizontal root density distribution. Horizontal growth stops in the middle of the inter-row, and competition between crop rows is not allowed in this model.

Model simulations

For testing the significance of parameter values, model simulations were run for 110 days starting from 1 April, with typical Danish weather conditions averaged for the period 1960-1990. Precipitation/irrigation was set according to evapotranspiration, to ensure a minimum downward percolation of nitrate during the crop growth period. Soil texture was selected so that it did not restrict the root penetration rate and root distribution. The default parameter values in the root module are shown in the list of abbreviations and the method was tested with form parameter value a_z ranging from 0 to 8. The effects of root penetration rate K_{rz}, and N uptake efficiency *kN* were also studied. To do so, the model was run with settings of K_{rz}=90% of default value (0.0009 m DD^{-1});

and S_r=90% of the default value (270000 m kg^{-1} DW). In addition, the root depth extension value was tested by setting values of q=1.3 (default) and q=1.0.

Sensitivity analysis

A sensitivity analysis was carried out for three different parameters in the root model. These were the sensitivity of the root depth penetration rate (k_{rz}), which controls how fast the roots occupy a new soil layer and soil depth for roots distributed with the logarithmic function; the specific root density (S_r), used to calculate the root length in each soil unit influencing the potential and actual N uptake; and the root zone extension depth (q), which is the extra root zone where root density declines linearly below the simulated rooting depth. These three parameters were tested with a range of values for the form parameter in order to test their different influence on plant N uptake.

Comparison against experimental data

Values of soil N depletion and root density distribution produced by the model were compared with the results from two field experiments, one including variable N supply for a white cabbage crop and the other comparing N dynamics in short rotation sequences including crops with very different root growth.

In the first experiment white cabbage was transplanted on 18 April and harvested on 21 October 2004. Soil mineral N was measured on 12 May and 26 October 2004. For this study we selected five of the fertiliser levels (A-E) included in this experiment, represented by Y_1:Y_2, where Y_1 was the N application in the preceding year (2003) to a cauliflower crop, and Y_2 was the N application on 18 May 2004 (kg mineral N ha^{-1}). The treatments were: A: 0:0, B: 230:0, C: 0:120, D: 230:120 and E: 390:120. No N application in 2003 (Y_1=0) resulted in low mineral N content in spring, whereas the two higher levels of N application in 2003 left high residual N levels in the subsoil.

Therefore this experiment is ideal for testing the ability to simulate deep root growth and N acquisition for this root model. The experiment is unpublished but information about soil and location has been reported elsewhere (Thorup-Kristensen 2006a). Simulated mineral N depletion of soil was tested with different a_z values of the white cabbage root model and compared with measured data from this experiment. Crop parameters adopted in simulations were *ddglag* 100, Kr_z 0.0014. In the simulation, the values 0, 1, 1.5, 2, 3, 4, 5, 6, 7, and 8 were tested for parameter a_z. Measured N uptake at harvest was compared with the a_z parameter. Measured soil mineral N values from the spring were used as initial conditions in the simulations and measured mineral N contents in late October in soil layers 0.0-1.0 m and 1.0-2.0 m were then compared with the values predicted by the model.

The validity of the model was also tested against data from another field experiment with three different vegetable crops representing shallow-rooted with low root density (leek), deep-rooted with medium root density (red beet) and deep-rooted with high root density (white cabbage). Leek, red beet and white cabbage were grown after a ryegrass catch crop or no catch crop in the preceding autumn, with two replicates, and the experiment was repeated in two years. Dry matter and N uptake were measured at harvest and mineral N in the soil was measured on 18 May and 31 October 2001 and 16 May and 30 October 2002. Detailed descriptions of the experiments have been reported elsewhere (Thorup-Kristensen, 2006a). Crop parameters adopted in the simulations were: *ddglag* 200, Kr_z 0.0004, a_z 8, a_x 8 for leek, *ddglag* 250, Kr_z 0.0009, a_z 2, a_x 2 for red beet, and *ddglag* 100, Kr_z 0.001, a_z 1.5, a_x 1.5 for white cabbage. Measured soil mineral N values from the spring were used as initial conditions in the simulations and measured mineral N contents in late October in the soil layers 0.0-1.0 and 1.0-2.0 m were used to compare with the predictions. Soil characteristics, weather data and crop management were as described in Thorup-Kristensen (2006a).

Statistical analysis:

Statistical analyses were conducted to evaluate the performance of the model in predicting soil mineral N using the Root Mean Square Error (RMSE) approach. RMSE was calculated as shown in equation 7. Here O_i was the observed value in the field experiment and P_i was the value predicted by the model, both with units (kg N ha^{-1}) and with n number of observations.

Equation 7 $$RMSE = \sqrt{\sum \frac{(O_i - P_i)^2}{n}}$$

Results

Root density distribution

Figure 1 shows the rooting depth after 110 days, equal to 1400 DD and assuming a q = 1.3. Figure 1 also shows root length distributions obtained from different values of the form parameter a_z. With form parameter a_z = 0, the roots were distributed evenly in the soil profile to the current simulated rooting depth, while a_z > 0 gave an exponential decline in root density with depth. When a_z > 3, the majority of the roots were found close to the soil surface. The fraction of root density in the extended zone (controlled by q) where root density decreases linearly with depth was high when a_z = 0 compared with that calculated with higher a_z values.

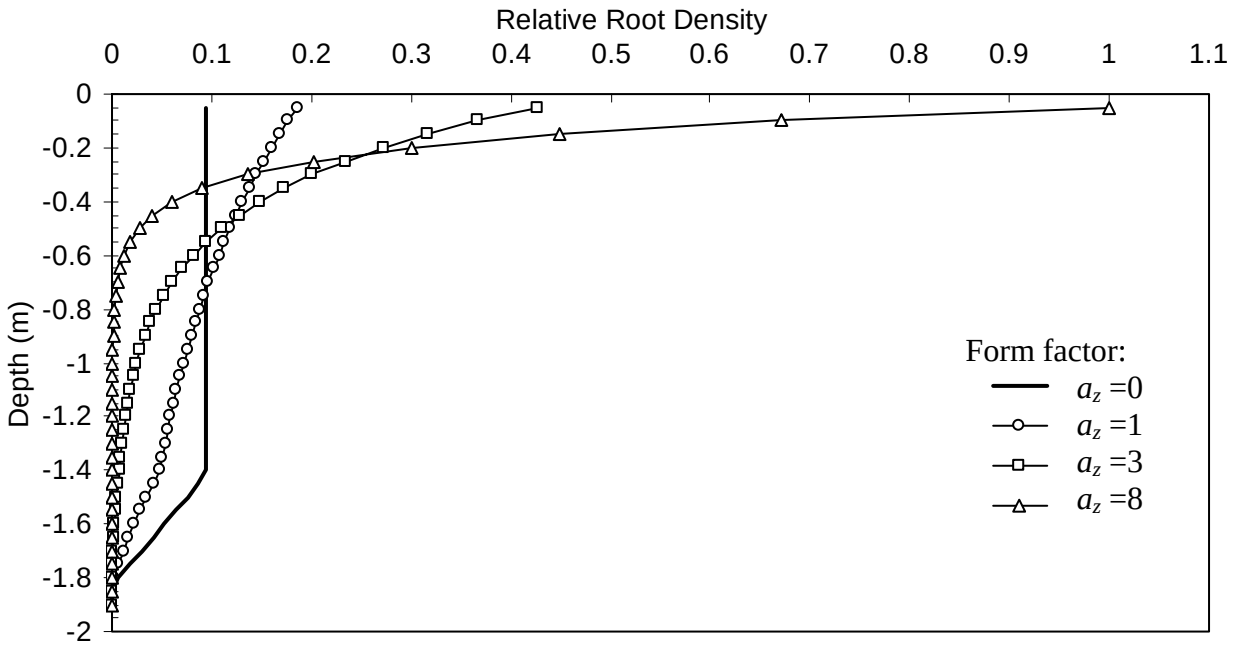


Figure 1. Relative root density distribution in soil profile for a root model simulation after 110 days with different values of a_z. Total root length is the same in all simulations. Default setting of root parameters include q =1.3. Key to symbols within diagram.

N uptake

In situations where the mineral N level in the topsoil was lower than the plant N demand, the form parameter had a significant impact on N uptake and soil N depletion. Figure 2 shows model simulations with different form parameter values and their impacts on soil mineral N depletion and relative plant N uptake. The value a_z=0 resulted in fast N uptake and the highest N depletion in the soil. The form parameter value a_z=1 resulted in slightly slower N uptake and depletion than a_z=0, whereas a_z=3 resulted in less N uptake and less depletion. The form parameter a_z=8 showed the lowest N depletion in soil and therefore a relatively low N uptake compared with a_z=0. The relative increase in N uptake at day 45 with form parameter a_z=3 and 8 (Figure 2B) was a result of

increasing root density and N uptake from deeper soil layers, layers which had already been depleted at this time by crops with form parameter values of a_z=0 and 1.

Soil N depletion occurred rapidly when roots reached the 0.25-0.5 m soil layer when a_z=0, 1 or 3, whereas a form parameter a_z=8 led to a rather slow depletion of this layer (Figure 3A). In the 1.0-1.25 m soil layer, a_z=0 and 1 still led to rather fast depletion, but depletion was slower for a_z=3 and a_z=8, where the fractions of N uptake compared to a_z=0 were only 0.52 and 0.01 respectively at the end of season (Table 1). Simulations where soil N content exceeded crop N demand (Figure 3B) showed similar differences, but against a background of generally much less efficient soil N depletion. While high a_z values led to low subsoil root density, they increased topsoil root density and N uptake capacity. In this case, a test showed that when 40 kg N ha^{-1} were added as fertiliser on day 90 in the first soil layer, 99% of this was taken up within two days with a_z=8, while it took 12 days with a_z=0.

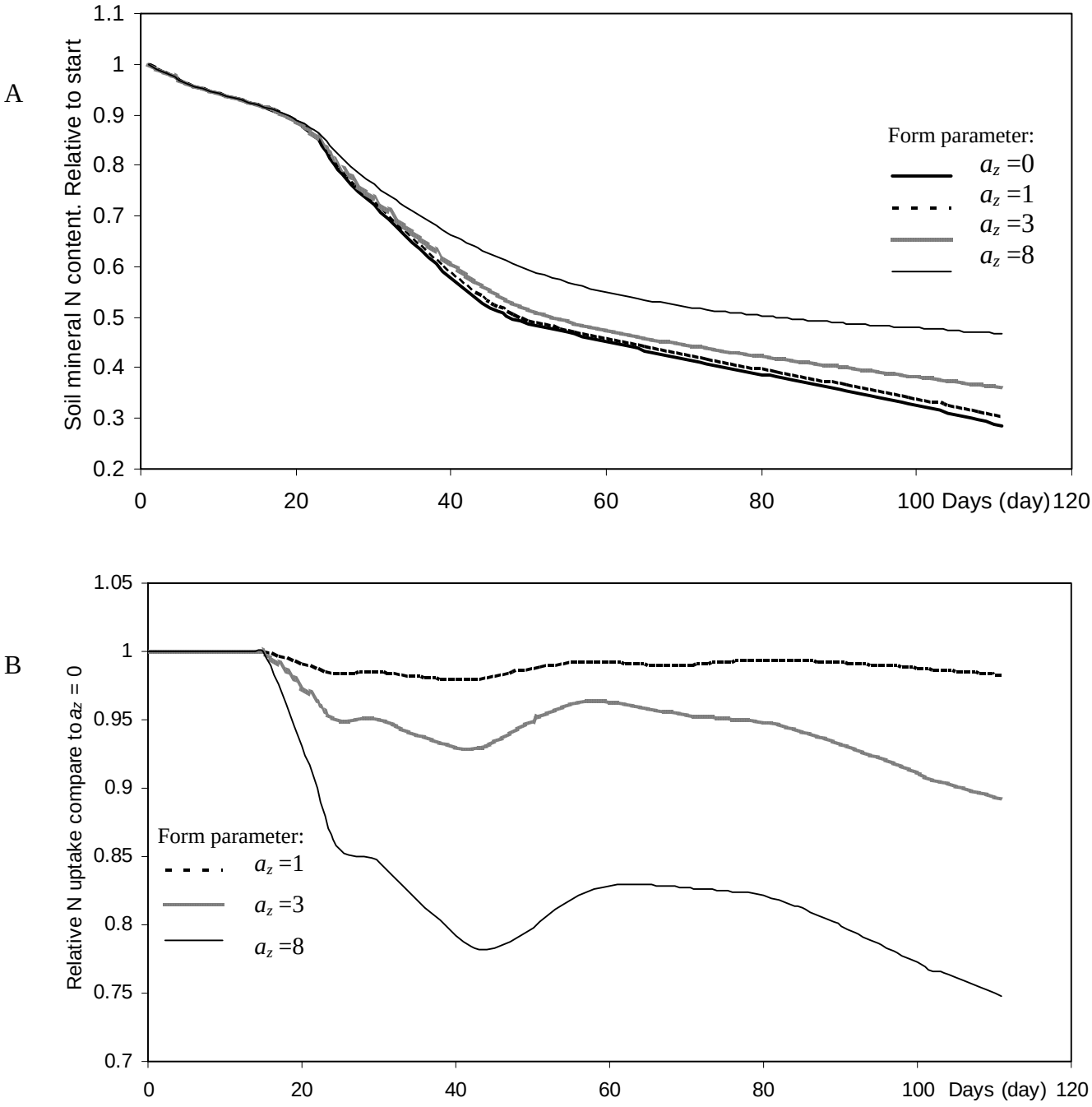


Figure 2. A) Relative soil N content in 0-2.0 m soil layer compared with initial soil mineral N content for form parameter a_z=0, 1, 3 and 8 for default root model simulation in a situation where soil N level was below potential plant N uptake. B) Relative N uptake in 0-2.0 m soil layer for form parameter a_z=1, 3 and 8 compared with N uptake for form parameter a_z=0 for default root model. Key to symbols within diagram.

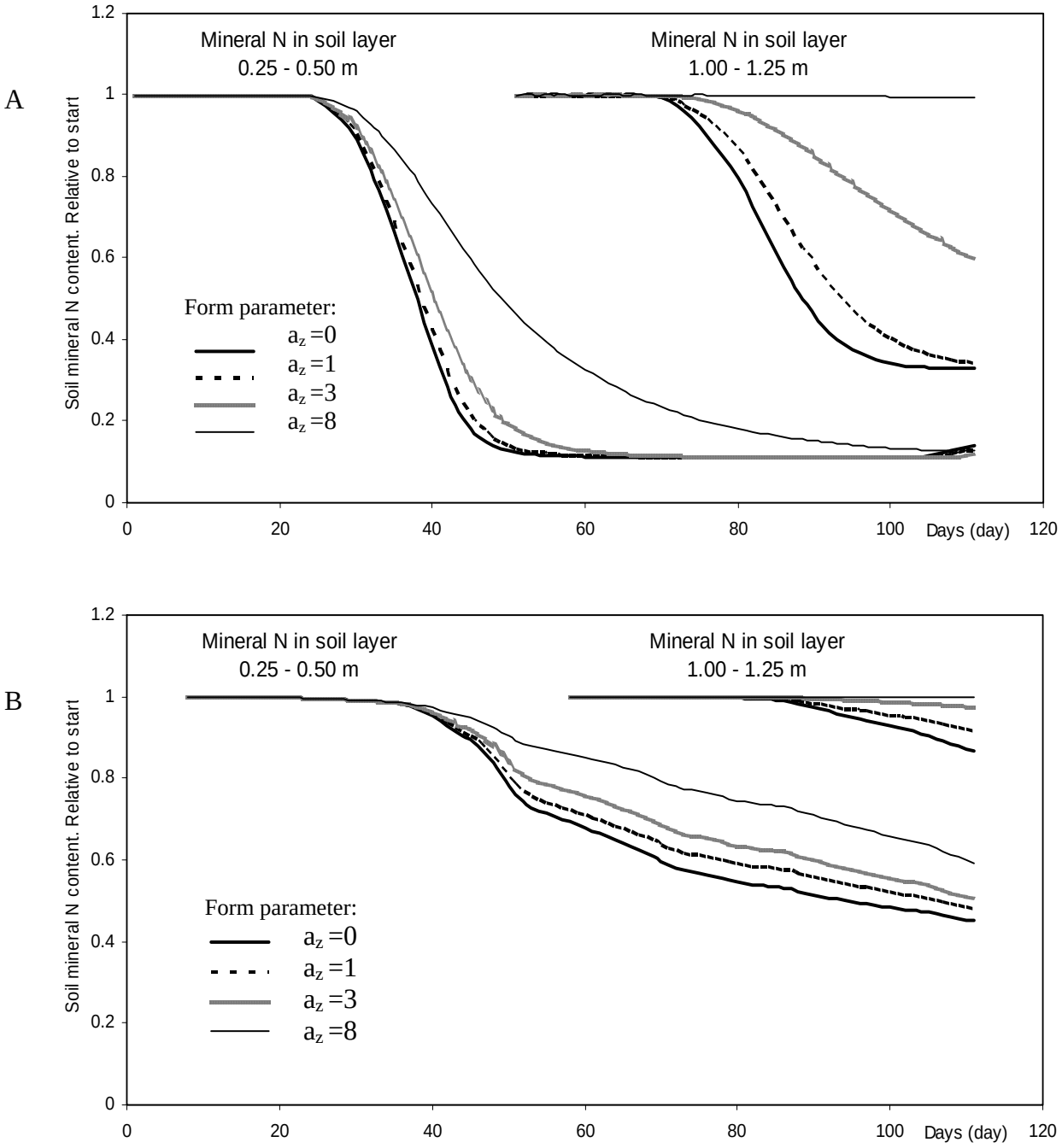


Figure 3. Soil mineral N content, relative to initial start concentration for default root model for form factor a_z=0, 1, 3 and 8 in 0.25-0.50 m and 1.00-1.25 m soil layers. A) Low N conditions, below potential uptake for the root model. B) High N conditions, corresponding to potential N uptake for the root model. Key to symbols within diagram.

Table 1. Relative plant N uptake in the 1.0-1.25 m soil layer. Simulation with the default model settings and simulation for testing model sensitivity for root penetration rate, specific root length and root extension

Form parameter a_z	**Default parameter setting** Fraction of plant N uptake 1.0 – 1.25 m	**Model sensitivity** Relative fraction in 1.0-1.25 m soil layer compared with the default setting (a_z =0…8, column two) of the model		
		$K_{rz90\%}$	$S_{r90\%}$	q=0
0	1	0.98	1.00	0.94
0.5	0.99	0.96	0.99	0.91
1	0.96	0.93	0.98	0.87
2	0.80	0.86	0.96	0.78
3	0.52	0.81	0.93	0.71
5	0.12	0.77	0.90	0.67
8	0.01	0.76	0.89	0.68

Sensitivity analysis

With form parameter value a_z=0, 1 and 3, plant N uptake from deep soil layers interacted with root penetration rate, because with these a_z values the crop had the potential to produce high root densities in deep soil layers (Figure 4A). With a_z=8 N uptake was less sensitive to root penetration rate (Figure 4A), as the root density in the deeper soil layers was very low in any case. N uptake in the 1.0-1.25 m soil layer was reduced by the delay in depth penetration, by a reduction factor of 0.93 to 0.98 with a_z <2. With a_z=3 or 8 the relative reduction was larger, with fractions of 0.81 and 0.76 respectively (Table 1), but as the actual uptake was much lower when a_z was high, the effect on absolute uptake was negligible at a_z=8.

Plant N uptake was dependent on the specific root length parameter (S_r). When S_r was reduced to 90%, an effect on N uptake was observed in the early stages from day 0 to day 50, but with no obvious effect later on for any of the a_z values (Figure 4B). Reducing specific root length S_r to 90% restricted plant N uptake from the 1.0-1.25 m soil layer by 11% with a_z=8, while minor to no effects were observed for lower a_z parameters (Table 1).

Similarly to root penetration rate, the root zone extension factor q had a larger effect on the relative N uptake during the simulation with form parameter value a_z=0 and less effect with a_z=3 than with a_z=8, where a small effect was simulated during early growth but disappeared during later growth (Figure 4C). The effect of using q=0 rather than the default value (q=1) reduced the relative N uptake in the 1.0-1.25 m soil layer by 32% and 6% for a_z=8 and a_z=0 respectively (Table 1), but in absolute terms, the effect was again negligible for a_z=8 but larger at a_z=0. We also tested the effects of variables $S_{r90\%}$ and $K_{r90\%}$ in the extended rooting zone (data not shown), and found that they were relatively small compared with the effect of variable a_z.

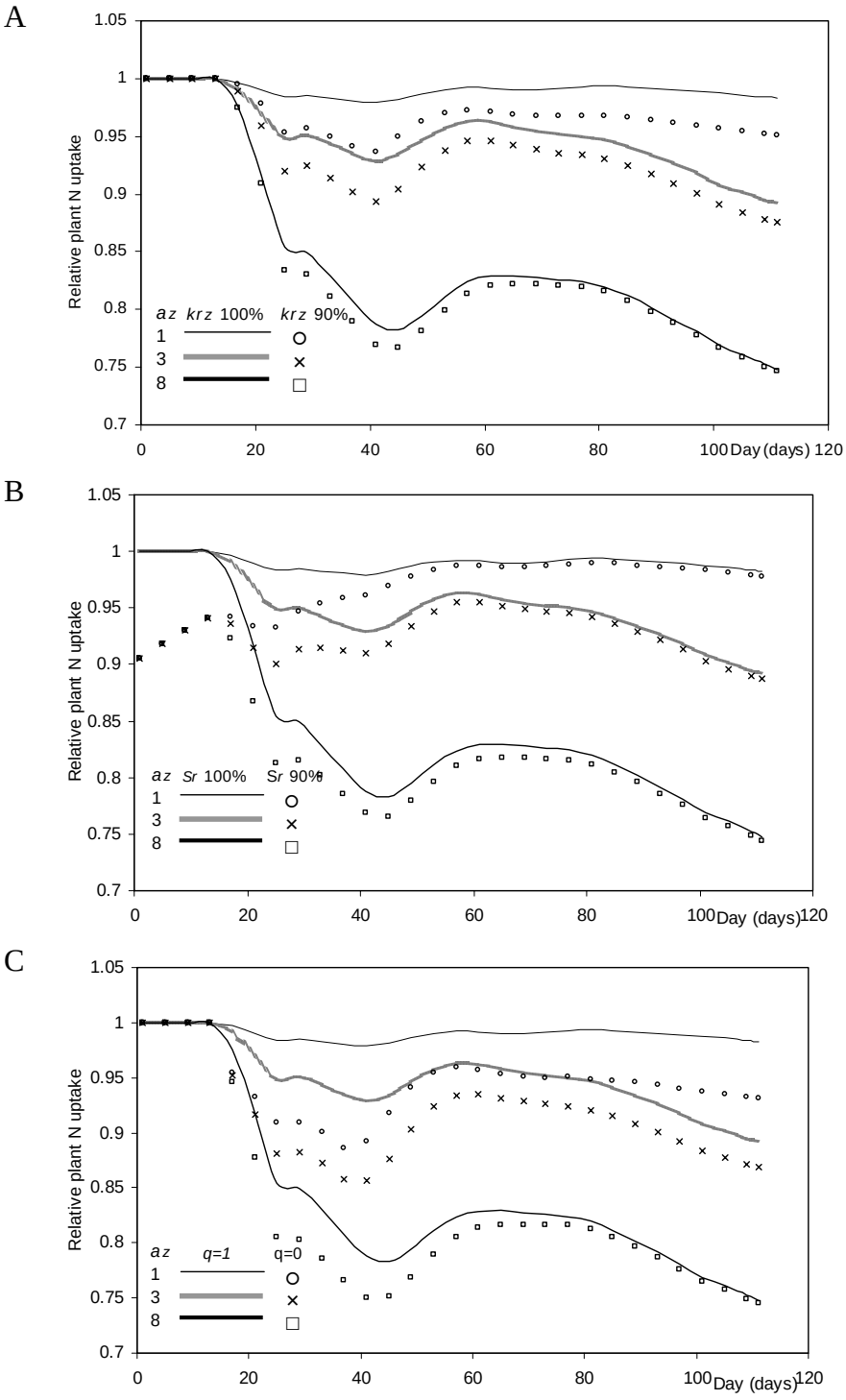


Figure 4. Default model settings compared with three different parameter settings. Relative N uptake for default form parameter a_z=0 compared with form parameter a_z=1, 3 and 8. A) Reduced root penetration rate (Kr_z) to 90% default settings. B) Reduced specific root length (S_r) to 90% of default settings. C) Simulation with and without linear root part (q=0). Key to symbols within diagram.

2-D simulation

Figure 5 shows simulated 2-D root density in a soil profile with three different a_x values for a crop grown with a row width of 1.0 m. Simulations with the form parameter values a_z=3 and a_x=0 showed high root density in the surface layer and distributed density evenly across row and inter-row soil. When a_x was increased to 3 or 8, the root density below the crop row became higher than the root density between rows.

Figure 6A shows N depletion with three different row widths. A root system simulated with a_z=3 depleted the soil N by 50% of the total mineral N content in the 0.25-0.5 m layer within 40 days and had consumed all available soil mineral N by day 60. These values changed to days 50 and 75 for a row width of 0.5 m and (a_z;a_x) (3;3), and days 60 and 100 for a row width of 1.0 m (Figure 6A). The effects of horizontal form parameter on root N uptake and soil N depletion for a row width of 0.5 m appeared to be minimal under the present conditions (Figure 6B).

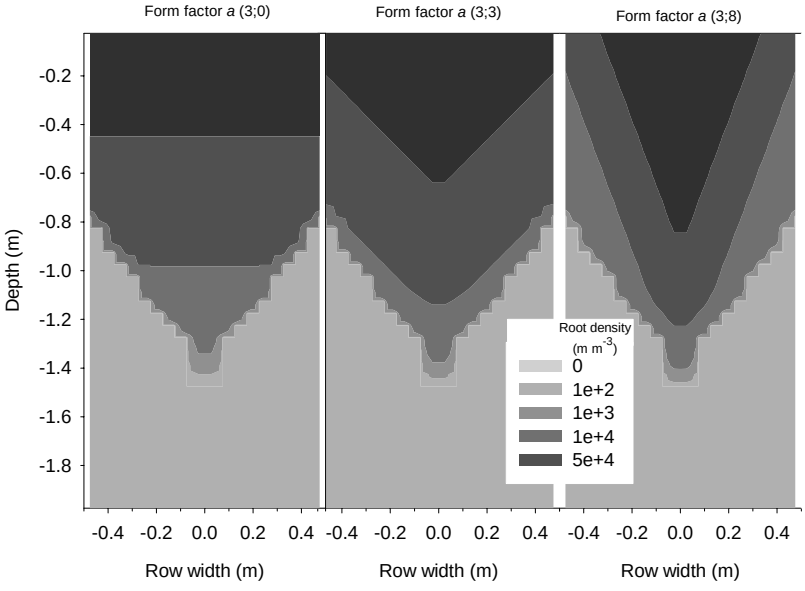
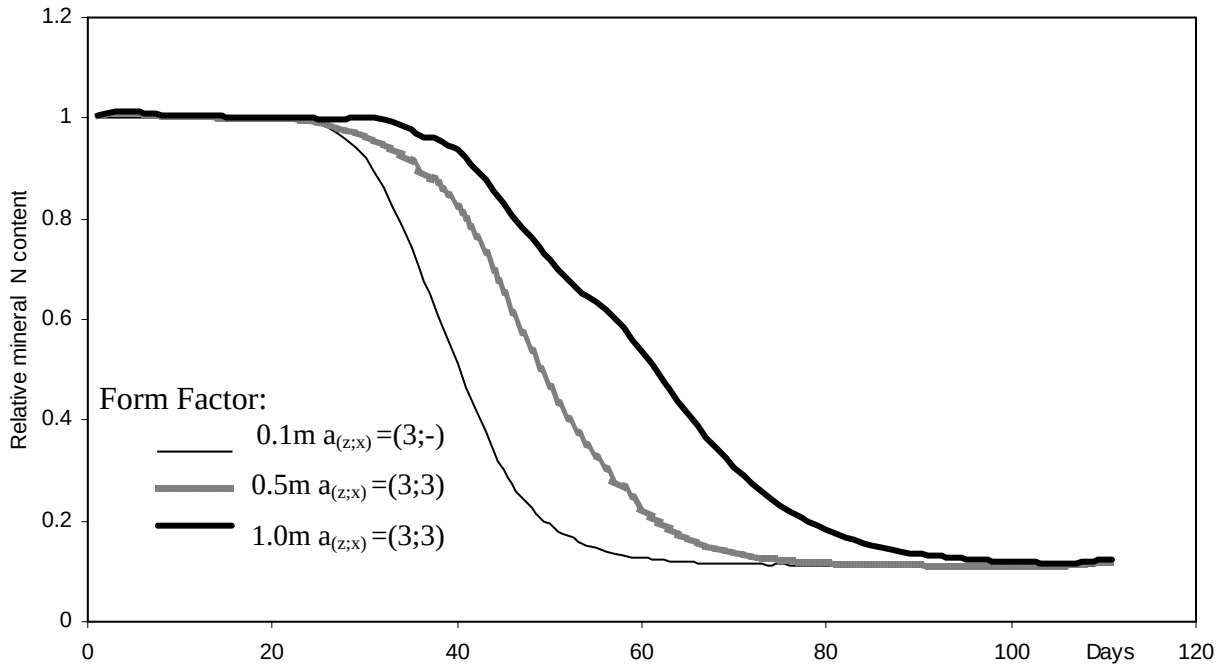


Figure 5. Root density in the soil profile in a 2-D system. Three different form parameter settings were used in 2-D: (a_z;a_x), (3;0), (3;3), (3;8). Decreasing root density is indicated by decreasing intensity of shading, see colour scale in figure.

A



B

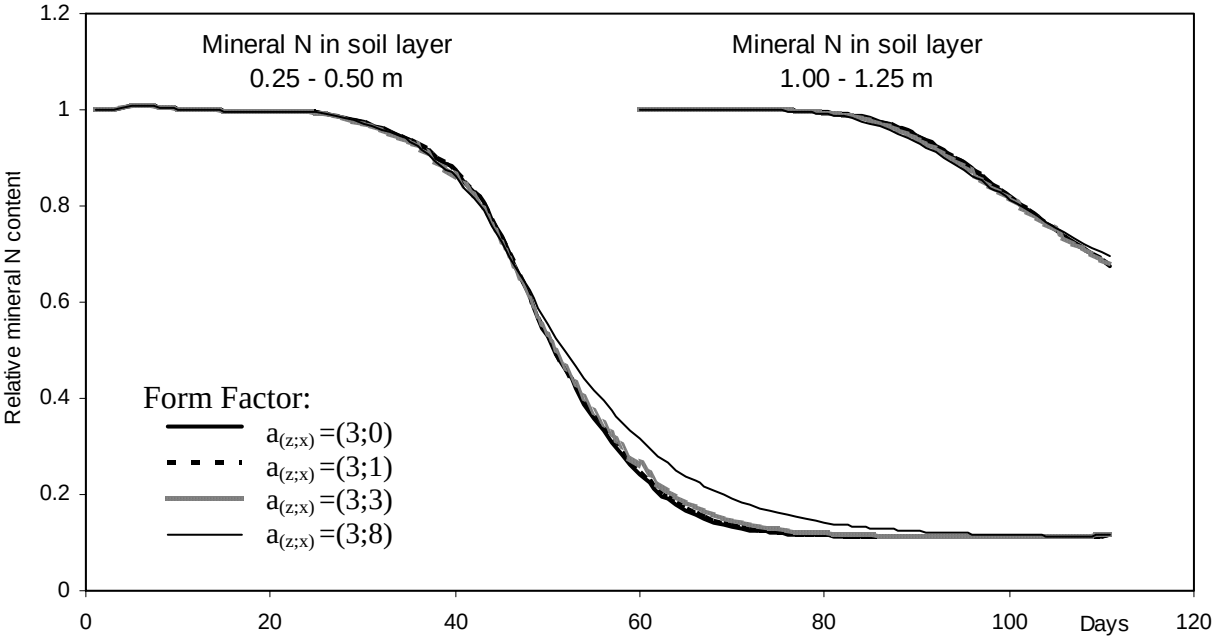


Figure 6. Soil mineral N content relative to initial value for the default root model. A) Relative mineral N content in 0.25-0.50 m soil layer. Form parameter a_z=3 into depth and width with three row widths. (Row width 0.1 m is calculated as 1-D) B) 0.5 m rows, form parameter a_z=3 into depth and 0, 1, 3 and 8 into width. Relative mineral soil content for two soil layers (0.25-0.50 m and 1.0-1.25 m) in a system with low mineral N content. Key to symbols within diagram.

Model comparison against field experimental data

The value of the form parameter a_z for simulating root distribution was tested against data from the field experiments. The distribution of roots into depth in the simulations accurately matched root data for white cabbage observed with minirhizotrons for days 46 and 64 with a_z=1.5 (Figure 7AB), whereas the root distribution in the minirhizotrons for day 153 and the simulated pattern did not fit well (Figure 7C). Modelled root distribution with use of form parameter a_z=0 to 1.5 had a significant part of the roots below 1.0 m, and in this way they mimicked the field data to some extent. Simulation of significant root density below 1.0 m is needed to replicate field results on plant N uptake.

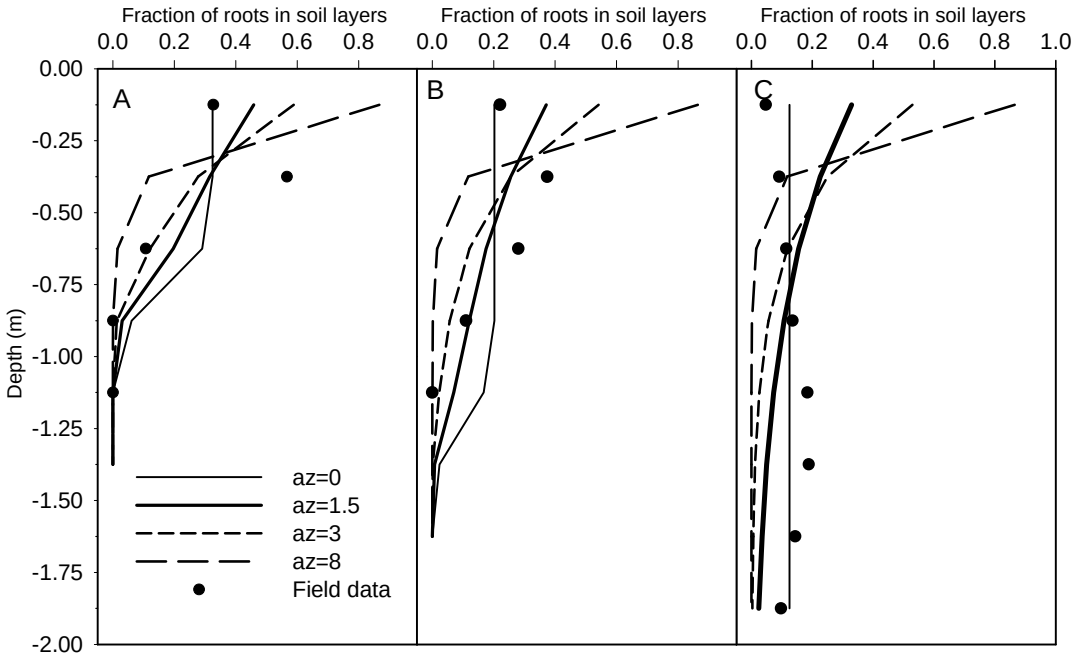


Figure 7. Comparison of field root intensity with simulated data of form parameter a_z. Root intensity in the field was measured at harvest as root intersection of grid in minirhizotrons below white cabbage crop and the fraction is calculated in 0.25 m soil layers in A) 46, B) 64 and C) 153 days after planting of white cabbage. Measured data are an average of five fertiliser levels with 3 replications. Simulated data are root density shown as relative root density distribution in soil layers. Form parameters a_z=0, 1.5, 3, and 8 are shown and a_z=1.5, which gave the best mineral N depletion in the soil layers is shown with the bold line.

When the plant available N was below plant N uptake capacity and some soil mineral N was found in deeper soil layers, crop N uptake was reduced at high a_z parameter values, and predicted N uptake was below field observations, as illustrated with fertiliser levels A and B in Figure 8A. When high N levels were found in the 0-1.0 m soil layer, plant N uptake in the simulations corresponded to field data and was not sensitive to the a_z value, as illustrated with fertiliser levels D and E. Mineral N content in soil layers was highly affected by the different a_z values (Figure 8B,C). For fertiliser levels A, B and C, the model depleted the 0-1.0 m soil layer more than indicated by field data. At harvest the soil contained very little N, although field data showed a higher N concentration in the topsoil layer than simulated data. The model accurately predicted mineral N content in the 1.0-2.0 m soil layer for a =0 to 2, indicating that simulation of a high root density at depth is needed to deplete this soil layer.

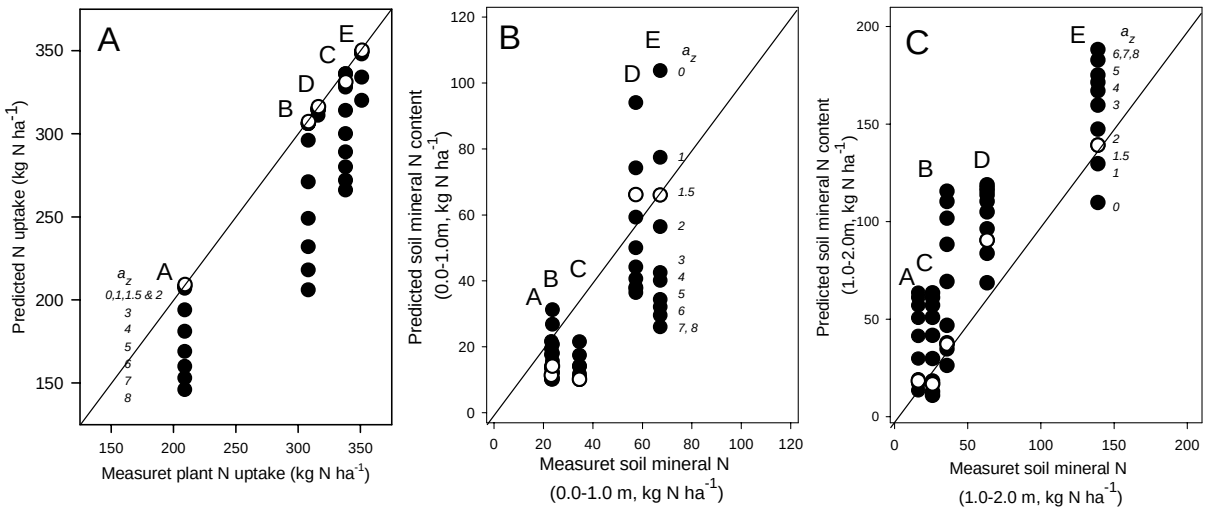


Figure 8. Comparisons of field experiments with white cabbage and different model options for form parameter a_z. A) Mineral N uptake for five different fertiliser levels tested with form parameter from a_z=0 to 8 (for fertiliser levels see Materials and Methods). Open symbols a_z=1.5, filled symbols see figure for a_z=0, 1, 2, 3, 4, 5, 6, 7 and 8, where a_z=8 showed lowest N uptake. B) Measured against model-predicted data for soil mineral N in the 0-1.0m soil layer. C) Measured against model-predicted data for soil mineral N in the 1.0-2.0 m soil layer. For fertiliser levels see figure. Open symbol a_z=1.5.

The simulated depletion of the 0.0-1.0 m soil layer was too low with a_z=0, leading to a high RMSE value for predicted mineral N level (Figure 9), whereas a_z values from 1 to 2 showed the best fit and lowest RMSE value. In the subsoil layer from 1.0 to 2.0 m, a_z=1 to 2 produced low RMSE values, whereas simulations with a_z=3 to 8 resulted in too low simulated N uptake, which resulted in higher RMSE values (Figure 9).

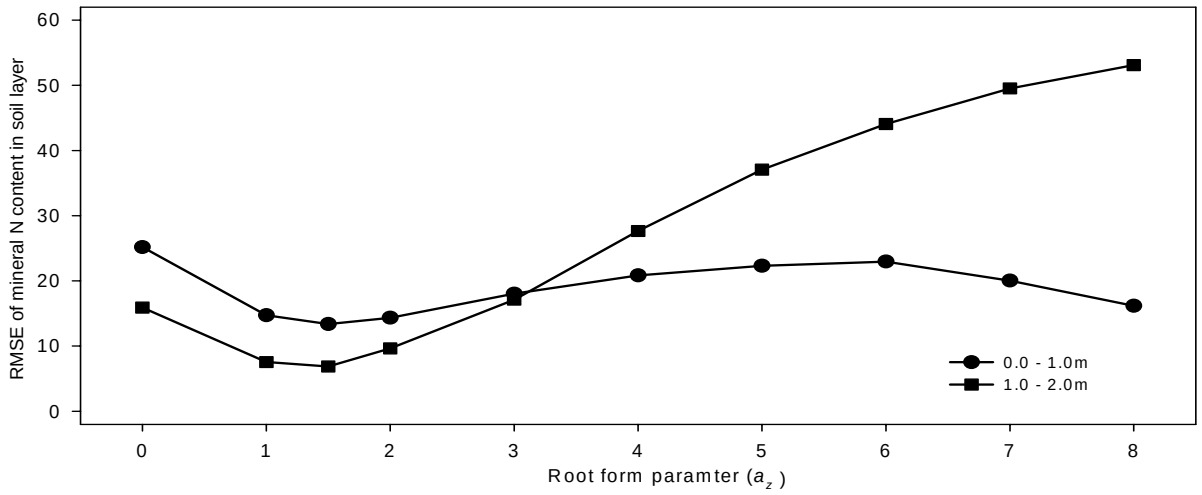


Figure 9. RMSE of predicted mineral N in soil layer for different values of form parameter a_z for simulations shown in Figures 8B and 8C. Circle = symbol for data 0-1.0 m depth, box = symbol for soil layer 1.0-2.0 m depth.

When observed root distribution of three vegetable crops was compared with simulations, the simulations of the leek root system matched observed data well, where a high root density was found in the surface layer and an exponential decrease, as for the root model with a_z=8 (Figure 10). Red beet and white cabbage crops showed high root intensity in the whole soil profile in the field where the root model had a_z=2 and 1.5 for red beet and white cabbage respectively, resulting in a lower partitioning of the root density in deep soil layers (Figure 10). The simulated soil mineral N content after the three vegetable crops following either a ryegrass catch crop or no catch crop in the previous autumn was correlated with field observations in the 0-1.0 m and 1.0-2.0 m soil layers

(Figure 11A,B). The simulations covered three different root systems and the catch crop effect, leading to variation in total soil mineral N content and variation in depth distribution of this.

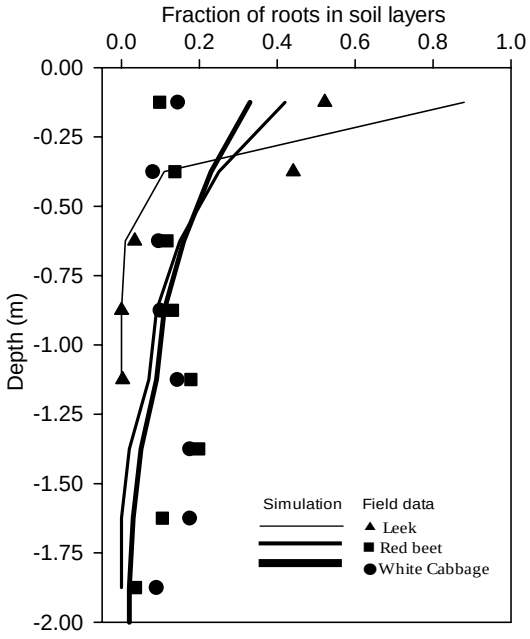


Figure 10. Comparison of field root intensity with simulated data for three vegetable crops. Root intensities in the field were measured on 5 September 2001 and 9 September 2002 for leek, and white cabbage as root intersections of grids in minirhizotrons below white cabbage crop and fraction is calculated in 0.25 m soil layers. Field data are an average of 2 years and 2 replications. Simulated data are root density shown as relative root density distribution in soil layers. Form parameter for leek was a_z=8, Red beet a_z=2 and white cabbage a_z=1.5. Key to symbols within diagram.

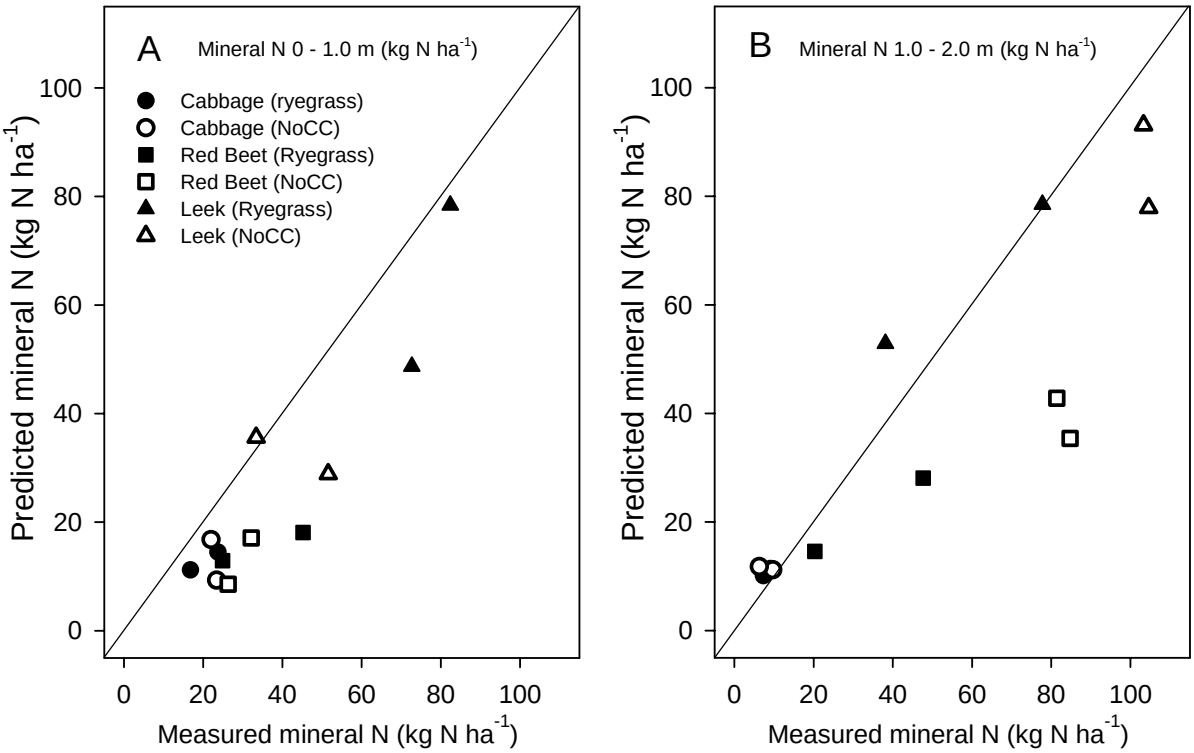


Figure 11. Comparison of measured and predicted data on mineral N in the A) 0.0-1.0 m and B) 1.0-2.0 m soil layer. Simulations of three vegetable crops with ryegrass catch crop (filled symbols) or no catch crop (open symbols) in the preceding year. The experiment was repeated in two years, shown here with identical symbols. Key to symbols within diagram.

With no catch crop, the N content in surface soil layer was low and subsoil N content was high. The model was able to simulate the effects of these different starting conditions, and their interaction with rooting depth of the three vegetable crops. Results revealed that leek only depleted the 0-0.5 m soil layer, due to its shallow root system, while red beet depleted the 0-1.0 m soil layer and white cabbage the whole 0-2.0 m layer for mineral N in the simulations, as well as in the field experiment. In the 0-1.0 m soil layer, the model underestimated soil mineral N content on the day of harvest by on average 33% or 10 kg N ha^{-1}. In the subsoil layer (1.0-2.0 m), the model overestimated N depletion for red beet in the simulations without catch crops, whereas the results for white cabbage simulations were in good agreement with the experimental data.

Discussion

Root penetration and density distribution

Rooting depth was calculated on the basis of day-degrees from air temperature, which is common for root models (Kage et al., 2000) and has been shown in field trials to be applicable to both monocot and dicot crops (Kirkegaard and Lilley, 2007; Smit and Groenwold, 2005).

The assumption of an exponential decrease in root length density with depth has been adopted in several models, with a fixed low root density at the calculated rooting depth, but a varying form factor to distribute increased root length mainly with increasing root density in the uppermost soil layers (Abrahamsen and Hansen, 2000; Barraclough and Leigh, 1984; Greenwood et al., 1982). This assumption has been shown to match monocots such as grasses and cereals reasonably well and was demonstrated here also for the vegetable crop leek, but not for dicot species such as oil radish or winter rape (Thorup-Kristensen, 2001a). In the model presented here, it was possible to vary the root length density in soil layers, especially in deeper soil layers with a fixed value of the form parameter but allowing root density to vary at calculated rooting depth. This variation in root distribution provides the opportunity to simulate a range of different crop species with significantly different root distribution. The model had problems simulating the deep root distribution of dicot species such as white cabbage in late season (Figure 7), but agreement was satisfactory in the earlier part of the growing season. Using an exponential equation for root density distribution only fully agrees with most monocot species and some dicot species. However, the purpose of this model was mainly to develop a root model where it was possible to alter crop N uptake in deeper soil layers compared with crop rotation models used today.

N uptake

The root model showed plant N uptake from the whole rooted zone, even when there was a high N level in the topsoil. Field experiments with high mineral N level in the topsoil layer also show some plant N uptake from deeper soil layers, indicating that this approach complies with field observations (Thorup-Kristensen and van den Boogaard, 1998). In a field experiment where sugar beet was grown, nitrate concentration was measured in three soil layers (0-0.2, 0.2-0.4 and 0.4-0.7 m depth) and these data showed a two-week delay in N depletion in the 0.4-0.7 m layer compared with the two layers above (Schmied et al., 2000). Furthermore, the two layers nearer the surface were depleted to the same soil N concentration at harvest, whereas the deepest layer had a higher soil N concentration. This delay in N depletion is also shown in Figure 3, where depletion of the 1.0-1.25 m soil layer began at day 75, depending on root penetration rate, and the efficiency of N uptake in this layer was dependent on the root density distribution, determined by a_z and plant N demand and mineral N level in soil layers above.

Depletion of mineral N down the soil profile was highly sensitive to the value of the form parameter. This makes the description of the root distribution very flexible and makes it possible to represent root systems from crops with very different distributions. Other parameters in the model was also analysed for sensitivity in N uptake. The root penetration rate was important for simulation of crops with low form parameters and high root densities at the calculated rooting depth. Depletion of mineral N below is sensitive to the q-parameter when the root density at the calculated root depth is high corresponding the low form parameters, but insignificant at low densities. In the beginning of the simulation the uptake of mineral N was sensitive to the specific root length, but the importance of this parameter degreased during the simulation. In the beginning of the simulation a 10% reduction in the specific rooting length resulted in a lower N uptake of 10%. However, this

reduction gradually decreased during the simulation to that after about 50 days, N uptake was only marginally influenced by the specific root length. This pattern was observed irrespective of the form parameter.

Comparisons between measured and simulated vegetable crops of leek, red beet and white cabbage showed that the model could be parameterized to simulate N depletion in 0-1.0 m and 1.0-2.0 m layers and matched the autumn level of mineral N in those two layers. Even with different soil mineral N levels in spring, the model predicted autumn soil mineral N level reasonably well, showing that the model could be parameterized to predict N depletion (Figure 9, 11) even if the modelled root distribution does not accurately comply with the root frequency distribution measured in the field (Figures 10).

Row crops such as carrots and maize have different rooting depth and root density below and between the crop rows. This root distribution leads to a lower N depletion in soil areas between rows, as has been demonstrated in field experiments (Liedgens and Richner, 2001a; Schröder et al., 1996; Thorup-Kristensen, 2006a). The model showed high sensitivity to row distance, but did not show high difference in N depletion with variation of the a_x form parameter. One explanation for this model behaviour was that the root penetration rate was relative high and the roots reached the middle of the row rapidly. Furthermore, with the rooting front in the deeper soil layers, the horizontal growth was limited or had just started so the a_x parameter had no effect. The 2-D model will be useful for simulating nitrate dynamics for row crops, for which the root systems have large differences between crop species. Furthermore, some vegetable crops are harvested as young plants in the vegetative phase with only a weakly developed rooting system, where it is important that the N supply reaches a valuable product. In those situations the model will be useful for predicting residual mineral N in 2-D soil profiles.

Conclusions

The root modelling approach taken in the present study involved simulating rooting depth, development and plant N uptake with only a few assumptions and the model can be paramatised to adapt the differences in root growth for vegetable and arable crops using only a few parameters, such as root form, lag phase for germination and root penetration rate. This model complied well with experimental data for monocot crops, whereas deep-rooted dicot crops were simulated with too low root density in the lower part of the rooting zone compared with observed data from experimental crops. However, by varying the a_z value, the model was capable of predicting N depletion in surface and subsoil layers reasonably well after crops with different N demand, rooting depth and depth distribution of the root system. 2-D root model was able to exploit root length and simulate N depletion both horizontal and vertically to comply with different row width and rooting depths.

Acknowledgements

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http://www2.warwick.ac.uk/fac/sci/whri/research/nitrogenandenvironment/eurotaten/

References

Abrahamsen P and Hansen S 2000 Daisy: an open soil-crop-atmosphere system model. Environ. Model. Soft. 15, 313-330.

Asseng S, Richter C and Wessolek G 1997 Modelling root growth of wheat as the linkage between crop and soil. Plant Soil 190, 267-277.

Barraclough P B 1989 Root growth, macro-nutrient uptake dynamics and soil fertility requirements of a high yielding winter oilseed rape crop. Plant Soil 119, 59-70.

Barraclough P B and Leigh R A 1984 The growth and activity of winter wheat roots in the field: The effect of sowing date and soil type on root growth of high-yielding crops. J. Agr. Sci. 103, 59-74.

Bloom A, Meyerhoff P, Taylor A and Rost T 2003 Root Development and Absorption of Ammonium and Nitrate from the Rhizosphere. Journal of Plant Growth Regulation 21, 416-431.

Brisson N, Gary C, Justes E, Roche R, Mary B, Ripoche D, Zimmer D, Sierra J, Bertuzzi P, Burger P, Bussiere F, Cabidoche Y M, Cellier P, Debaeke P, Gaudillere J P, Henault C, Maraux F, Seguin B and Sinoquet H 2003 An overview of the crop model stics. Eur. J. Agron. 18, 309-332.

Burns I G 1980 Influence of the spatial distribution of nitrate on the uptake of N by plants: A review and a model for rooting depth. J. Soil Sci. 31, 155-173.

Dunbabin V M, Diggle A J and Rengel Z 2002 Simulation of field data by a basic three-dimensional model of interactive root growth. Plant Soil 239, 39-55.

Forde B G and Lorenzo H 2001 The nutritional control of root development. Plant Soil 232, 51-68.

Gerwitz A and Page E R 1974 Empirical Mathematical-Model to Describe Plant Root Systems. J. Appl. Ecol. 11, 773-781.

Greenwood D J, Gerwitz A, Stone D A and Barnes A 1982 Root development of vegetable crops. Plant Soil 68, 75-96.

Greenwood D J, Rahn C, Draycott A, Vaidyanathan L V and Paterson C 1996 Modelling and measurement of the effects of fertilizer-N and crop residue incorporation on N-dynamics in vegetable cropping. Soil Use & Management 12, 13-24.

Greenwood D J, Rahn C, Draycott A, Vaidyanathan L V and Paterson C 2001 Modelling N-response of field vegetable crops grown under diverse conditions with N_ABLE: A review. Journal of Plant Nutrition 24, 1799-1815.

Hansen S, Jensen H E, Nielsen N E and Svendsen H 1991 Simulation of nitrogen dynamics and biomass production in winter wheat using the Danish simulation model daisy. Fertil. Res. 27, 245-259.

Kage H, Kochler K and Stützel H 2000 Root growth of cauliflower (Brassica oleracea L. botrytis) under unstressed conditions: Measurement and modelling. Plant Soil 223, 133-147.

Kirkegaard J A and Lilley J M 2007 Root penetration rate - a benchmark to identify soil and plant limitations to rooting depth in wheat. Aust. J. Exp. Agr. 47, 590-602.

Kohl M, Büttcher U and Kage H 2007 Comparing different approaches to calculate the effects of heterogeneous root distribution on nutrient uptake: a case study on subsoil nitrate uptake by a barley root system. Plant Soil 298, 145-159.

Kristensen H L and Thorup-Kristensen K 2004 Root Growth and Nitrate Uptake of Three Different Catch Crops in Deep Soil Layers. Soil Sci. Soc. Am. J. 68, 529-537.

Kutschera L 1960 Wurzelatlas mitteleuräischer Ackerunkrüter und Kulturpflanzen. DLG Verlag, Frankfurt-am-Main.

Liedgens M and Richner W 2001b Minirhizotron observations of the spatial distribution of the maize root system. Agron. J. 93, 1097-1104.

Liedgens M and Richner W 2001a Minirhizotron observations of the spatial distribution of the maize root system. Agron. J. 93, 1097-1104.

Nielsen N E and Barber S A 1978 Diffferences Among Genotypes of Corn in the Kinitics of P Uptake. Agron. J. 70, 695-698.

Pages L, Vercambre G, Drouet J-L, Leccompte F, Collet C and Le Bot J 2004 Root Typ: a generic model to depict and analyse the root system architecture. Plant Soil 258, 103-119.

Penning de Vries F W T, Jansen D M, ten Berge H F M and Bakeman A 1989 Simulation of ecophsiological processes of growth in several annual crops. Pudoc: Wageningen,The Netherlands.

Schmied B, Abbaspour K and Schulin R 2000 Inverse Estimation of Parameters in a Nitrogen Model Using Field Data. Soil Sci. Soc. Am. J. 64, 533-542.

Schröder J J, Groenwold J and Zaharieva T 1996 Soil mineral nitrogen availability to young maize plants as related to root length density distribution and fertilizer application method. Neth. J. Agr. Sci. 44, 209-225.

Smit A L and Groenwold J 2005 Root characteristics of selected field crops: Data from the Wageningen Rhizolab (1990-2002). Plant Soil 272, 365-384.

Smit A L and Zuin A 1996 Root growth dynamics of Brussels sprouts (*Brassica olearacea* var. *gemmifera*) and leeks (*Allium porrum* L.) as reflected by root length, root colour and UV fluorescence. Plant Soil 185, 271-280.

Thorup-Kristensen K 2001a Root growth and soil nitrogen depletion by onion, lettuce, early cabbage and carrot. Acta Hortic. 563, 201-206.

Thorup-Kristensen K 2006a Root growth and nitrogen uptake of carrot, early cabbage, onion and lettuce following a range of green manures. Soil Use Manag. 22, 29-39.

Thorup-Kristensen K and Van den Boogaard R 1998 Temporal and spatial root development of cauliflower (*Brassica oleracea* L. var. *botrytis* L.). Plant Soil 201, 37-47.

Thorup-Kristensen K 2001b Are differences in root growth of nitrogen catch crops important for their ability to reduce soil nitrate-N content, and how can this be measured? Plant Soil 230, 185-195.

Thorup-Kristensen K 2006b Effect of deep and shallow root systems on the dynamics of soil inorganic N during 3-year crop rotations. Plant Soil 288, 233-248.

Thorup-Kristensen K and van den Boogaard R 1998 Temporal and spatial root development of cauliflower (Brassica oleracea L. var. botrytis L.). Plant Soil 201, 37-47.

Thorup-Kristensen K and van den Boogaard R 1999 Vertical and horizontal development of the root system of carrots following green manure. Plant Soil 212, 143-151.

van Keulen H and Seligman H G 1987 Simulation of water use, nitrogen nutrition and growth of a spring wheat crop. Pudoc: Wageningen, The Netherlands.

Weaver J E 1926 Root development of field crops. McGraw, New York.

Xue Q, Zhu Z, Musick J T, Stewart B A and Dusek D A 2003 Root growth and water uptake in winter wheat under deficit irrigation. Plant Soil 257, 151-161.

Zuo Q, Shi J, Li Y and Zhang R 2006 Root length density and water uptake distributions of winter wheat under sub-irrigatio. Plant Soil 285, 45-55.